MICROCLIMATIC ASPECTS OF RETREAT SITE AND BASKING SITE SELECTION BY THE TASMANIAN TIGER SNAKE, *Notechis ater* sp. (Serpentes: Elapidae).

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This thesis is dedicated to those who, in the future, may wish to use the information therein for the benefit of the snake.

Abstract

The thermal ecologies of two elevationally isolated populations of adult female Tasmanian Tiger Snakes (*Notechis ater* sp.) were investigated using stomach implanted radiotelemetry and a comprehensive microclimate monitoring programme. The study sites were Egg Islands, in the Huon Valley in southeastern Tasmania, and at Lake Crescent, on the lower Western Central Plateau of Tasmania.

The study had four primary aims: (i) to determine the microclimatic conditions associated with retreat site and basking site selection; (ii) to record and compare behavioural thermoregulatory response to micrometeorological variation; (iii) to monitor diel rhythmicity and range of body temperatures; (iv) to determine voluntary thermal limits and eccritic body temperatures. This information was used in two ways: firstly, to identify the preferred physical microhabitat of this species; and secondly, to develop two predictive models of adult female Tiger Snake activity. The first is a relatively simple empirical model based on microclimatic correlates of body temperature; the second, a biophysical approach involving analysis of the snake's energy budget. Development of the first model required identification of those environmental parameters and quantities which: (i) trigger emergence; (ii) determine the amount of time necessary for the daily warm-up phase in differing micrometeorological conditions; (iii) allow the animal to move about within its home-range; and (iv) trigger entry into retreat sites. In order to develop the second model detailed information on body temperatures and on the pertinent microclimatic variables within the animal's immediate vicinity were required. It also required information on the physical dimensions and behavioural characteristics of the animal. In addition, other questions relating to the thermal ecology of this species are asked.

The determined correlates of body temperature and daily patterns of activity included total down-welling radiation, global radiation, ground surface temperature, ground heat-flux, and inground temperature. Cloud cover and wind direction were found to influence the snakes thermoregulatory behaviour.

The telemetry results, determined in a temperature gradient chamber, showed elevational differences in eccritic mean body temperatures and voluntary thermal limits of non-gravid females, but similar temperatures for gravid females. The field telemetry showed diel rhythmicity and the range of body temperatures for four Egg Island females which showed differences between gravid and non-gravid females.

The empirical model was found to explain daily activity and validate assumptions made necessary to develope the biophysical model.

The biophysical model is a modified integrated parameter model, based on empirical relationships, and was tested against the field telemetry derived body temperature data. The model was found to explain a minimum of 65% and a maximum of 84% of the variance desplaying a high level of significance. The results show that the snakes are optimising their thermal uptake.

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SYMBOLS

A	effective radiating surface area (m^2)
a	coefficient of the thermal expansion of a fluid (1/273 for a perfect gas)
C	total heat flux ($W\ m^{-2}\ s^{-1}$)
c	cloud cover (%)
Cp	specific heat capacitance ($J\ m^{-3}\ °C^{-1}$)
CT	critical thermal limit (°C)
D	diffuse sky radiation ($W\ m^{-2}$)
DA	dorsal surface area (m^2)
d	characteristic dimension (m)
dd	dorsal body wall thickness (m)
dv	ventral body wall thickness (m)
ds	vapour density of saturated air ($kg\ m^{-3}$)
da	vapour density of free air ($kg\ m^{-3}$)
dT	difference in temperature (°C)
dt	difference in time (s)
E	evaporation rate ($kg\ m^{-2}\ s^{-1}$)
g	gavitational acceleration ($9.81 ms^{1}$)
h	convective coefficient ($W\ m^{-2} s^{-1}\ °C^{-1}$)
h'	convective coefficient for a cylinder ($W\ m^{-2} s^{-1}\ °C^{-1}$)
H	heat flux rate ($W\ m^{-2}\ s^{-1}$)
hc	convective heat flux ($W\ m^{-2}$)
In	insulation ($m^2\ °C^{-1} W^{-1}$)
I	direct radiation ($W\ m^{-2}$)
k	thermal conductivity ($W\ m^{-1}\ °C^{-1}$)
k_a	thermal conductivity of free air ($W\ m^{-1}\ °C^{-1}$)
K	thermal conductance ($W\ m^{-2}\ °C^{-1}$)
K_e	overall thermal conductance ($W\ kg^{-1}\ °C^{-1}$)
$K_{e\,mod}$	modelled overall thermal conductance ($W\ kg^{-1}\ °C^{-1}$)
K_{es}	conductance value of a standard laboratory enclosure of operative temperature ($W\ kg^{-1}\ °C^{-1}$)
K_{sf}	conductance at the animal surface ($W\ kg^{-1}\ °C^{-1}$)
K↓	down-welling global radiation ($W\ m^{-2}$)
L	longwave radiation ($W\ m^{-2}$)
M	metabolic heat production ($W\ m^{-2}$)

Ms	snake mass (g)
Q*	net radiation received at the surface (W m^{-2})
Q_a	total amount of radiation absorbed (W m^{-2})
Q_{ad}	net radiation flux on the dorsal surface (J m^{-2})
Q_{al}	net radiation flux on the ventral surface (J m^{-2})
Q_C	rate of heat transfer due to conduction (W m^{-2} $°C^{-1}$)
Q_E	latent heat flux (W kg^{-1})
Q_{Er}	latent heat flux due to respiration (W m^{-2})
Q_{Eb}	latent heat flux at the body surface (W m^{-2})
Q_H	sensible heat flux (W m^{-2})
Q_G	ground heat flux (W m^{-2})
Q_n	net absorbed solar and thermal radiation (W m^{-2})
ΔQs	change to body heat store (°C)
r_b	boundary layer resistance to water vapour (s m^{-1})
r_c	cutaneous resistance to water vapour (s m^{-1})
R	radiant emittance (W m^{-2})
*R**	net radiant emittance (W m^{-2})
R	equivalent radiation conductance (W m^{-2})
RH	relative humidity (decimal fraction)
S	heat flux on each body part (W m^{-2})
ST	net heat flux on the sum of the body parts (W m^{-2})
s	second
T	temperature (°C)
T_a	air temperature (°C)
Tb	deep body temperature (°C)
T_{bm}	model body temperature (°C)
T_e	operative temperature (W $°C^{-1}$ m^{-2})
T_{es}	standard operative temperature (W $°C^{-1}$ m^{-2})
T_g	inground temperature (°C)
T_s	animal surface temperature (°C)
T_r	ground surface temperature (°C)
ΔT	temperature gradient (°C)
$\bar{u}$	mean wind speed at a height of 2cm (m s^{-1})
$\bar{U}$	mean wind speed at a screen height of 1.6m (m s^{-1})
V	mean wind direction (°)
VA	lateral surface area (m^2)
v	kinematic viscosity ($m^2 s^{-1}$)
VT	voluntary thermal limit (°C)
Z	zenith angle (°)

Z_o	roughness length (m)
α	albedo ($0 < \alpha < 1$)
αs	snake albedo ($0 < \alpha < 1$)
αr	ground surface albedo ($0 < \alpha < 1$)
ε	emissivity ($0 < \varepsilon < 1$)
εs	snake emissivity ($0 < \varepsilon < 1$)
εr	habitat emissivity ($0 < \varepsilon < 1$)
σ	Stephan-Boltzmann's constant ($5.673 * 10^{-8}$ W m^2 °K^4)
$\downarrow$	down-welling radiative flux (W m^{-2})
$\uparrow$	up-welling radiative flux (W m^{-2})
λ	latent heat of vaporisation (W kg^{-1})

ABBREVIATIONS

ASL	above sea-level
C.S.L.	central science laboratory
C.S.I.	Campbell Scientific Instruments
CT	critical thermal
EST	eastern standard time
EWL	evaporative waterloss
Gr	Grashof number
Nu	Nusselt number
S	sub site
SVL	snout/vent length
VT	voluntary thermal (temperature)

1 INTRODUCTION

Animals interact with their physical environments in complex ways which determine their distributions, behaviour, predator-prey interactions and feeding strategies. Our understanding of these relationships may be limited and the complexities involved necessitate a focal point. Gates (1975) considers that, as energy is a primary requirement of any animal, many of the relationships and responses can be addressed successfully through the unifying focus of energy exchange. Energy transfer between animals and their physical environments is a continuous and variable process influenced by the intrinsic properties of both. The relationship may vary with season, time of day and location, and involves physiological and behavioural responses to a geometrically and spectrally variable incident radiation.

Temperature is an important resource to animals living in cool environments, particularly in seasonally extreme areas, with relative importance increasing with increasing latitude and elevation. To a reptile, temperature is one of the most important components of its environment and it will spend a large part of each day responding to its thermal environment. Because reptiles rely primarily on external heat sources for growth, reproduction and maintainence activities, it is important when studying the ecology of any reptile to look at the various paths of heat exchange available.

The daily and seasonal activity patterns of reptiles are strongly influenced by their thermal requirements (Porter *et al.* 1973; Huey, 1982). Consequently, in studying the daily activity patterns of Tiger Snakes *(Notechis ater)*, attention will be focused on available thermal energy, rather than on food or chemical potential energy, and on the biological and physical exchange mechanisms acting in thermal energy transfer.

Thermoregulation in snakes has been studied less thoroughly than in lizards possibly due to their dangerous and secretive reputations, however, several recent studies have attempted to interpret the thermoregulatory behaviour of elapid snake species based on body temperature measures. These have included taking body temperatures from the cloaca with glass thermometers (Dredge, 1981; Schwaner, 1989), surgical implantation of radiotelemeters (e.g. Shine and Lambeck, 1990), and a few by force-feeding radiotelemeters (Shine, 1987b). Radiotelemetry studies have been conducted in four Australian snake families (Acrochordidae, Boidae, Colubridae and Elapidae) (Shine,1987b) and many have dealt with thermoregulatory behaviour. The current study differs from most previous work in this area in that it combines behavioural

observations of free-living snakes with a comprehensive evaluation of habitat microclimate. The results will allow for a meaningful interpretation of the thermal ecology of this species by identifying and quantifying the sources and sinks of thermal energy within each animal's home-range.

1.1 BIOPHYSICAL ECOLOGY, A MULTIDIMENSIONAL SCIENCE

Biophysical ecology is a subdiscipline of ecology which utilises an analytical approach towards understanding the interactions between the biotic and abiotic components of an ecosystem (Gates 1975, 1980). To this end, it applies mathematical and physical laws to the principles of biology. By definition, biophysical ecology assumes a reductionist approach, in contrast to a holistic one, towards ecology. It is a simplification which may lead to a neglect of other important aspects of an ecosystem; for example, competition for other resources besides energy, such as animal/plant interactions, trophic levels and predator/prey relations. Instead, it focuses on the energy/mass exchange mechanisms which serve to link lifeforms with their physical environments (Gates, 1980).

1.1.1 Defining biophysical mechanisms

In determining the energy budget of an animal the physiological, behavioural and physical mechanisms of energy exchange need to be addressed. The sources and sinks of thermal energy available to a terrestrial vertebrate include metabolism, radiation, convection, conduction, and the latent heat of evaporation (Gates 1975, Campbell, 1977). Each of these affect an animal's energy balance. The principal climatic factors simultaneously interacting on most terrestrial animal energy budgets include radiation, air temperature, wind and vapour pressure.

In the context of animal/thermal environment interaction the animal and its physiological and behavioural adjustments are considered the dependent variables on the largely independent climate. Thermoregulation is a dynamic and multifaceted process in which the animal attempts to achieve or maintain a body temperature, within a thermal zone, in response to actual or anticipated change to heat load; and it is dependent on ecological and physiological factors (Huey, 1982).

In the current study it is intended that an appropriate evaluation of snake/environment energy interaction will allow determination of the microclimatic conditions influencing adult female Tasmanian Tiger Snake activity during summer. However, only the behavioural and physical mechanisms of energy-exchange are considered here and the physiological mechanisms must remain for future research.

1.2 THE TASMANIAN TIGER SNAKE

The Tasmanian Tiger Snake is a large proteroglyphic terrestrial snake belonging to the family Elapidae. All proteroglyphs have relatively short non-rotating fangs and typically neurotoxic venoms, and include the most dangerous snakes in the world. Following the classification and nomenclature used by Gow (1976) and Cogger (1983), the Tasmanian Tiger Snake (*Notechis ater humphreysi*) is a subspecies of *Notechis ater* (Krefft, 1866), however, the relationships of the various sub-species (currently four) are obscure and the subject is contentious and will not be entered into here. The genus is generally confined to southern Australia and *N. ater* is widely distributed, occurring in the Flinders Ranges, in south-western West Australia, on south-eastern South Australia offshore Islands, and on many islands of Bass Strait and in Tasmania.

In Tasmania the species grows in excess of 1.5m and is often melanotic or dark brown with banded individuals common in some areas. The live-born young are sometimes strongly banded, particularly from the lowland areas, and are generally more cryptic than adults. The Tasmanian Tiger Snakes are diurnal and at certain times may be observed foraging in the middle of the day. Diet may vary with the age of the snakes; when young readily feeding on tadpoles, frogs, skinks and even fish, and as adults they will hunt small birds and mammals. Body size determines the size of prey taken.

The Tiger Snake in Tasmania occurs from sea-level to above 1200m elevation. Habitat is varied and includes: dry sclerophyll woodland, rocky outcrops, creek margins, marshland, tussock grassland, farmland, alpine and coastal heathland, and dune areas. The species is commonly associated with the borders between open areas and dense cover; and at higher elevation with dolerite outcrops and especially those with a northern aspect. Dredge (1981) considers Tiger Snakes to be absent from Tasmanian rainforest and wet sclerophyll and to be largely confined to drier areas within the state.

The writer undertook a survey of annual sightings of snakes in Tasmania in 1991 and the results for the 1990 sightings of Tiger Snakes are given in Fig.1.1. The data show the peak of activity to occur in February and a minimum of activity in July (the coldest month); however, these data are for the State as a whole and activity varies depending on local conditions and elevation.

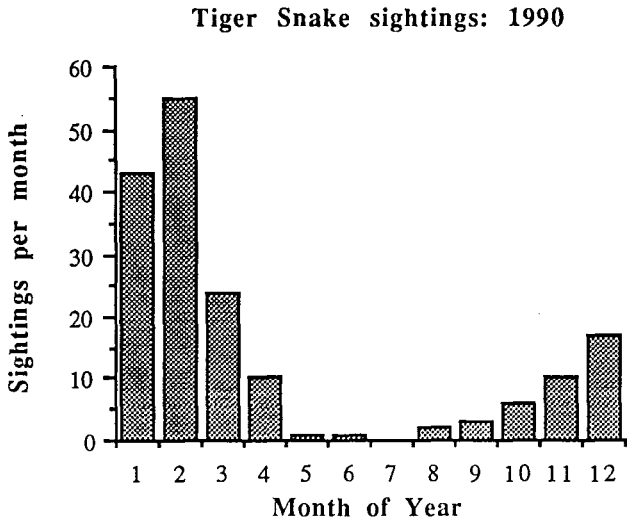


Fig. 1.1 Tiger snake sightings for 1990, Tasmania state wide.

1.3 OBJECTIVES AND JUSTIFICATION OF RESEARCH

The primary aims of this study are fourfold: (i) to determine the microclimatic conditions associated with retreat site and basking site selection; (ii) to record and compare behavioural thermoregulatory response to micrometeorologic variation; (iii) to monitor diel rhythmicity and range of body temperatures; (iv) to determine voluntary thermal limits and eccritic body temperatures. In this study the four primary aims are investigated for two elevations within the State during the summer season 1992/93.

This information will be used in two ways: firstly, to identify the preferred physical microhabitat of this species; and secondly, to develop two predictive models of adult female Tiger Snake activity. The first, a relatively simple empirical model based on microclimatic correlates of body temperature; the second, a biophysical approach involving analysis of the snake's energy budget. Development of the first model requires identification of those environmental parameters and quantities which: (i) trigger emergence, (ii) determine the amount of time necessary for the daily warm-up phase in differing micrometeorological conditions, (iii) allow the animal to move about within it's home-range, (iv) trigger entry into retreat sites. In order to develop the second model detailed information on body temperatures and on the pertinent microclimatic variables within the animal's immediate vicinity are required. It also requires information on the physical dimensions and behavioural characteristics of the animal; i.e. exposed surface area, surface albedo, body-wall thicknesses, thermal conductance, and behavioural mechanisms of thermoregulation.

1.3.1 Questions

The present study asks if it is possible to model Tiger Snake activity patterns based solely on microclimatic parameters and energy budget analysis in Tasmania, and if these models are adequate for predicting Tiger Snake behaviour.

A study of this kind will also suggest other questions relevant to the thermal ecology of this species and although answering these questions is not central to the theme of this study they are nonetheless pertinent to an understanding of Tiger Snake thermal ecology. The more obvious of these are given below:

Optimising thermal environments

Do Tasmanian Tiger Snakes make optimum use of their thermal environments? For example, will they minimise exposure to wind while maximizing exposure to solar radiation during their daily warm-up phase? Do they bask in exposed positions only for the time necessary to elevate body temperatures to optimal levels? To what depth do they go within retreat sites at night in summer and do they select locations in retreat sites that maximise body heat retention?

Elevational differences

Are the voluntary thermal limits of two elevationally isolated populations of Tiger Snakes different in Tasmania? Do they exhibit different selected body temperatures at elevational extremes that favour maximal seasonal activity and does this explain observed differences in activity patterns? Are Tiger Snakes at higher elevation less likely to travel long distance to reach suitable basking sites, than are those at lower elevation, in response to a cooler and less predictable environment?

Sexual and asexual differences

Are females more closely associated with a particular home-range than males outside of the mating season in Tasmania? Do the largest females hold the thermally optimal sites? Do gravid females thermoregulate more precisely than non-gravid females, and to what extent do optimal body temperatures and activity patterns of gravid females differ from non-gravid females?

Answers to the above questions are relevant for predicting activity patterns based on microclimatic parameters in this species and, therefore, have been included in the discussion.

STRUCTURE

Chapter two outlines the biological considerations necessary to understand the thermal ecology of animals in general with an emphasis on reptiles, as an introduction to the study. Chapter three describes in detail the theory of energy exchange and the main models available for animal energy budget analysis, and then introduces the integrated parameter model used in this study. Chapter four describes the regional setting and the study sites. Chapter five details the methods and materials used in data aquisition. Chapter six analyses the data obtained and discusses implications arising from the data and relationships within the measured variables. The animals are found to behave within simple biophysical limits, selecting sites which maximise their thermal opportunity. Some previously used predictors of animal body temperature are shown to be unsuitable. Chapter seven integrates the information into predictive models of Tiger Snake behaviour, relating behaviours to meteorological conditions. Various relationships are presented which describe the thermoregulatory behaviour within a physically coherent framework which allows for future improvements of our understanding of the animals themal ecology. The thesis concludes by summarising the findings of the study and suggests directions for further research.

2 BIOLOGICAL CONSIDERATIONS

2.1 THERMAL BIOLOGIES

"The thermoregulatory activities of animals are nearly as varied and complex as the terminology devised by students of thermoregulation to describe those activities"

(Pough and Gans, 1982, p. 17)

2.1.1 Introduction

Some confusion exists in the literature regarding relevant terminology and, in light of the problem, this chapter aims to provide working definitions of the biological terms used throughout this thesis together with a brief overview of the thermal strategies utilised by animals. The following focuses on reptiles, however, reference is made to other vertebrate groups where pertinent and where information on reptiles may be lacking.

Animals are termed endothermic, if they have physiological mechanisms for maintaining internal temperatures within narrow limits (±2°C or less, Bligh and Johnson, 1973) independent of ambient temperatures (i.e. homoiothermic or 'warm-blooded'). Animals are termed ectothermic if they lack physiological temperature control mechanisms and their body temperatures fluctuate with that of their surroundings (i.e. poikilothermic or 'cold-blooded'). Both homoiotherm and poikilotherm are arbitrary distinctions of internal thermal state based on stable laboratory conditions. The use of the term ectotherm (Cowles, 1940) is here considered more appropriate than poikilotherm in describing those cold-blooded animals capable of thermoregulation through behavioural response to an external heat-source ('behavioural homoiotherms'). Animals with a wide temperature tolerance are termed eurythermic, while others with only a very narrow tolerance are termed stenothermic.

Between the extremes of thermoconforming ectotherms and thermoregulating endotherms, animals exhibit varying degrees of thermoregulatory ability (Whittow, 1970). Even within a species seasonal switching of thermal-strategy may occur, from thermoregulator to thermoconformer and visa-versa (such animals may be termed heterothermic). Many reptiles (considered ectotherms) are capable of withstanding

energy shortages during winter by allowing deep body temperature (Tb) to fall near ambient, some as low as 1-4°C (Schmidt-Nielsen, 1983). Thermoconforming animals in winter are said to be hibernating (most vertebrates that hibernate are small), while in a state of physiologically maintained inactivity, or in torpor. However, physiological inactivity may also occur in animals in summer (aestivation).

In general, the daily activities of ectotherms are determined far more by the thermal characteristics of their environments than are those of endotherms (Gans and Pough, 1982); for example: resource utilization, competition and habitat partitioning (Ruibal and Philibosian, 1970; Huey and Slatkin, 1976; Huey and Webster, 1976; Huey, 1982). Endotherms, however, are generally less responsive to small scale fluctuations in their physical environments and the dependency on microclimatic parameters may be less obvious.

Endothermal heat production does occurs in reptiles (Bartholomew, 1982), but it is of a much lower magnitude than in homoiotherms, and may afford such species limited independence of microclimatic constraints (e.g. brooding pythons). Reptiles are not 'cold-blooded' in the sense that diurnal body temperatures of freely moving reptiles are equal to that of their environment; reptile body temperatures are often elevated over environmental temperatures and maintained within narrow limits by a complex of physiological and behavioural adjustments.

2.1.2 Defining body temperature

No single temperature actually defines the Tb of a terrestrial vertebrate (Pough and Gans, 1982) as heat is unevenly distributed throughout the body. In this discussion Tb refers to the deep (or core) body temperature. In a snake the elongated and flexible body form may result in regional differences in Tb due to the animal occupying several microhabitats at the same time. For these reasons it is important to standardize any method of measuring Tb's so that the results obtained will permit accurate interpretation of the thermal status of different animals. In practice animal Tb's may be taken from the oesophagus (Dredge, 1981), stomach, deep rectum or cloaca (Schwaner, 1989), depending on the species; or by the more sophisticated method of radiotelemeter implantation into a body cavity. However, oesophageal, rectal or cloacal sites may not be representative of true core temperatures and are easily influenced by handling (e.g. Castilla and Bauwens, 1991). There are difficulties not only in defining Tb but also in accurately determining mean Tb values. In light of this, and in view of the lack of standardized methods employed by many researchers a degree of caution is necessary when evaluating the literature.

As the body core temperature is defined as: "The mean temperature of the tissues at a depth below that which is affected directly by a change in the temperature gradient through the peripheral tissues" (Bligh and Johnson, 1973, p. 944) the term is considered inappropriate for small to medium ectotherms, as their body temperatures are affected directly by changes in temperature gradient. Consequently, the term 'deep body' temperature may more accurately define the body temperatures of reptiles (Pough and Gans, 1982).

2.1.3 Temperature range

Generally, terrestrial animals have Tb's which can vary greatly from environmental temperatures. Reptiles differ in the range of temperatures they can tolerate and these ranges may also differ with time. The Tb range tolerated by endotherms is generally much less than that tolerated by ectotherms. All reptiles have a Tb range associated with activity, termed the 'activity temperature range' (Pough and Gans, 1982), within which they may engage in maintenance activities and where there exists an optimum temperature (or temperatures) for physiological function. The activity range is delimited by voluntary thermal limits (VT_{min} and VT_{max}) which are selected by the animal. In ectothermal vertebrates this implies selected or 'preferred' body temperatures. However, while it is correct to say that ectotherms select preferred temperatures, when allowed to by environmental conditions, it is incorrect to assume that there is a single optimum environmental temperature for metabolic processes. Selected temperature is not fixed, but may vary with time, hormonal, and physiological state (Dill, 1972; Garrick, 1974; Hutchison and Kosh, 1974; Lang, 1981; Lillywhite, 1980; Patterson and Davies, 1978; Regal, 1966, 1967, 1980; Shine and Lambeck, 1990). Selected Tb's in reptiles have been recorded to vary even on a daily basis (Regal, 1967; Hutchison and Kosh, 1974). For this reason the term eccritic (Gk. *ekkrinein*, to select) temperature is commonly used as a synonym for selected Tb. Reptiles also have extended Tb ranges defined by critical thermal limits (CT_{min} and CT_{max}) beyond which animals will eventually die; i.e. though not considered to be physiologically lethal, the CT may be ecologically lethal in animals unable to find shelter (Pough and Gans, 1982). CT_{max} is probably the most widely used correlate of temperature for activities in reptiles (Huey, 1982). VT_{min} and VT_{max} are the points at which the animal seeks heat or shelter. In the ectotherm a basking range occurs between VT_{min} and the activity range. A thermoregulating reptile may only tolerate extension of its activity range by incurring energetic expense through physiological and/or behavioural compensation.

2.1.4 Acclimatisation

The limits of thermal tolerance are dependent on a reptiles's previous thermal history. Reptiles are capable of physiologically extending their CT ranges if new environmental temperatures are approached gradually and experienced over extended periods; such animals are then considered to have acclimatised to the new temperature. Change in temperature tolerance may occur in response to climate change and under natural conditions can prepare the animal for survival during periods of extreme temperature. Available information suggests that there is no clear understanding of the physiological mechanisms involved in modification of the CT range (Schmidt-Nielsen, 1983). It is known however that metabolic enzyme systems play an important role (Hochachka and Somero, 1973) in that biochemical processes, in which the rates of reaction may vary by two to four times for every 10°C variation in Tb (also referred to as the Q10), somehow compensate to newly experienced temperatures (Schmidt-Nielsen, 1983). Thus biochemical thermal sensitivity may vary as a function of thermal history of the animal. Natural acclimatisation is an important environmental adaptation as in many highland areas in Tasmania seasonal temperature change can be extreme and during winter animals may tolerate temperatures that if experienced during summer may be lethal.

2.1.5 Evaluating animal response

Because previous thermal history determines thermal tolerance it is important, when looking at animal/temperature regime response, to know the thermal history of the animal in question. This can be achieved through habituation of the animal to a specific temperature under laboratory conditions; a process known as acclimation, which will allow for a more accurate interpretation of animal response to a particular range of temperatures. This is important because one cannot know the extent to which environmental temperature is limiting activity without having first determined the eccritic temperature, activity range and the VT (or CT) limits of the animal under controlled conditions. Physical environments will, on occasion, prevent reptiles from achieving eccritic temperatures (Licht *et al.*, 1966; DeWitt, 1967; Porter *et al.*, 1973; Huey and Webster, 1976; Muth, 1977; Magnuson *et al.*, 1979). In practice the animal's response to a laboratory controlled temperature gradient is determined only after it has had sufficient time to acclimate to the artificial temperature. In ectotherms it may be as short as 24 hours or as long as 20 days (Schmidt-Nielsen, 1983). Alternatively, if the reptile is to be evaluated based on the current field conditions, the temperature response should be determined as soon as is practicable after capture in order to avoid acclimation to the artificial temperature regime.

2.2 FACTORS INFLUENCING TEMPERATURE REGULATION

2.2.1 Photoperiod

Homoiotherms are known to experience regular daily Tb fluctuations which are entrained to daily light cycles (e.g. Rose, 1985), but are independent of exogenous thermal cues. Diel Tb cycles in reptiles, though governed by photoperiod in at least some lizard families (e.g. Anguidae, Agamidae, Iguanidae and Scincidae) and dependent on a functional parietal organ (Stebins, 1963; Hutchison and Kosh, 1974; Avery, 1979; Heatwole and Taylor, 1987), are usually not independent of exogenous thermal regimes. Thus, a meaningful interpretation of Tb in reptiles, when applied to microclimatic data, will require additional information concerning normal activity patterns as functions of time and date of sampling.

2.2.2 Cost-benefit of thermoregulation

Metabolic rate varies directly with Tb and, as such, any change in Tb will incur metabolic cost (Huey, 1982). Similarly, locational change and postural adjustments require energy expenditure (Avery, 1982). These costs need to be determined when assessing the net benefit of thermoregulation (Huey and Slatkin, 1976). In theory, cost-benefit models predict that precise thermoregulation will be beneficial only if associated costs are low; i.e. physiologically optimal benefit can only be ecologically optimal if the energetic costs and risk of predation are minimal (Huey and Slatkin, 1976; Hainsworth and Wolf, 1978; Magnuson et al., 1979; Huey, 1982). From the above, the predicted energetic costs for a thermoregulating reptile would be low when associated with open habitats, and high in heavily shaded or forested habitats; however, the risk of predation may override these considerations. Hence, many reptile species may thermoconform (be non-baskers), or be less precise thermoregulators (Lee, 1980), when associated with dense vegetation (high energy cost habitats), or when occurring in tropical zones (Huey and Slatkin, 1976; Huey and Webster, 1976). These and other cost-benefit considerations (e.g. time, social interactions, competition, food availability) may collectively determine thermal strategy and thermoregulatory precision. An accurate thermal map of the home range (body or environmental temperature) is important for quantifying thermoregulatory costs, and for facilitating a meaningful interpretation of Tb and associated behaviour.

2.2.3 Surface area:mass ratio and heat storage capacity

The surface area:mass ratios of reptiles affect their thermoregulatory behaviour by

influencing the rates of energy exchange with the environment. As surface area:volume ratio varies inversely with mass the surface areas of small animals are relatively large. Further, as heat exchange with the environment (via radiation, convection, conduction and in part evaporation) occurs at the animal's external surface, the potential rate of heat exchange with the environment in small animals is relatively great. The elongate body form and relatively large surface area:mass ratios of snakes is associated with substantial energy cost in endotherms (Schmidt-Nielsen, 1983). In the Mustelidae, which display an elongate and narrow body form, heat exchange, when outside of the thermal neutral zones, is approximately double that of more conventional shaped mammals of comparable size (Brown and Lasiewski, 1972). When a snake's body is extended the increased and relatively high surface area to mass ratio will allow for a rapid rate of heat exchange, and when tightly coiled will minimise this exchange (Bartholomew, 1982). The low mass specific metabolic rates of reptiles may help explain why so many lizards are small; as small ectotherms need not spend much energy thermoregulating. The limited heat storage capacity of small reptiles means that they are track the immediate thermal conditions more closely than larger animals.

Body heat storage capacity is a function of body mass and specific heat. The average heat capacity (Cp) of living protoplasm is approximately 3.43 J g^{-1} $°C^{-1}$ (Bartholomew, 1972) and is Tb dependent; the exact value may vary interspecifically and even intraspecifically (Schmidt-Nielsen, 1983).

2.2.4 Limited endothermy

Limited endothermy occurs in some reptiles, especially the larger species (Bartholomew and Lasiewski, 1965; Bartholomew *et al.*, 1965; Bartholomew, 1982), and large to medium sized reptiles may warm-up faster than they cool (Heatwole and Taylor, 1987). This latter characteristic has been shown to be absent in experiments on dead animals (Bartholomew, 1982), indicating physiological thermal control, however, in smaller reptiles the rates of heating, or cooling, may be reversed in forced convective situations (Fraser and Grigg, 1984). Endothermy, while characteristic of all mammals, can vary in magnitude (Dawson and Grant, 1980). The basal metabolic rates of both endotherms and ectotherms are labile; for example the rates of active varanid lizards can overlapping those of inactive mammals (Bartholomew, 1982; Pough and Gans, 1982).

2.2.5 Limited insulation

In contrast to endotherms, small ectothermic vertebrates characteristically lack insulative

coverings. Fat as an insulating material, while peripherally minimal in ectotherms, may be considered superior to exterior insulation in that heat transfer through it to the surface of the animal is under homeostatic control via blood flow to the periphery. The thermal conductivity (k) of fat (0.205 $Wm^{-1}°C^{-1}$, Gates, 1980), when compared to soils or to lizard skin (0.502 $Wm^{-1}°C^{-1}$, Porter and Gates, 1969), is relatively low and therefore it has a relatively high insulation value (though this is largely a function of density). Air also has a low k and can be influential in energy transfer. However, since reptiles may possess only limited ability to trap air next to the body surface (in the uncoiled position), the importance of air as an insulative layer to these animals may be minimal.

2.2.6 Variation in body temperature

Terrestrial reptiles may vary eccritic Tb's in response to: season (in snakes: Carpenter, 1956; Hirth and King, 1969; Gibson and Falls, 1979; Schwaner, 1989; Shine and Lambeck, 1990), digestive state (Regal, 1966; McGinnis and Moore, 1969; Cogger, 1974; Gatten, 1974; Witten and Heatwole, 1978; Bradshaw et al., 1980; Bozinovic and Rosenmann, 1988; Schwaner, 1989; pers. obs.), health (pers. obs.), gender (Schwaner, 1985; Shine and Lambeck, 1990), and reproductive status (Schwaner, 1989). Such observations have led some investigators (Lang, 1979; Pough, 1980) to postulate that reptiles (and amphibians) may have multiple physiologically optimal temperatures (Huey, 1982).

Seasonal shifts in Tb have been interpreted as a response to changing physical environmental constraints (Lillywhite, 1987) or as resulting from an inverse relationship between eccritic and acclimated temperatures (Scott and Pettus, 1979). However, the cost of thermoregulatory behaviour, in terms of energy, time and risk of predation, may offset any energy gains to be accrued from the behaviour (Huey and Slatkin, 1976).

2.2.7 Thermoregulatory precision in reptiles

Not all reptiles thermoregulate precisely while active (Ruibal, 1961; Heatwole, 1970; Rubial and Philibosian, 1970; Hertz, 1974; Huey 1974a, b, 1982; Huey and Webster, 1975, 1976; Lee, 1980). Thermoregulatory precision has been demonstrated to be influenced by environmental heterogeneity (Soulé, 1963), weather (Licht *et al.*, 1966), time of day (Regal, 1967), food availability (Swingland and Frazier, 1979), competition and predators (DeWitt, 1967; Regal and Connolly, 1980).

Imprecise thermoregulation and eurythermy may increase potential activity periods and thus outweigh the advantages of precise thermoregulation and stenothermy (Huey, 1982).

2.2.8 Activity periods in reptiles

Limits to potential daily and seasonal activity periods in reptiles are primarily determined by thermal and moisture (hydric) characteristics of the habitat (Bartlett and Gates, 1967; Porter and Gates, 1969; Porter *et al.*, 1973; Tracy, 1982) and by the characteristic biologies of the species (Huey, 1982). Time of activity may be further limited by food and water availability (e.g. Porter *et al.*, 1973; Huey and Slatkin, 1976), competition (Magnuson *et al.*, 1979), predation (McFarland, 1976), gender and reproductive status (Rose, 1981; Schwaner, 1989; Shine, 1991; Shine and Lambeck, 1990). Interspecific differences in activity times are more commonly seen in reptiles than in endotherms (Schoener, 1977) and the activity periods of most reptiles are comparatively short, especially in temperate zones (Avery, 1979). The annual activity periods of lizards have been shown to be negatively correlated with altitude (Huey, 1982). However, not all individuals in a reptile population are likely to be active every day even in ideal weather conditions (Bradshaw *et al.*, 1980).

Huey (1982) considers that there are two themoregulatory strategies available to sequestered reptiles: (i) they may select thermally buffered retreat sites which afford them warm and stable microhabitats (Heatwole, 1970; Porter *et al.*, 1973; Huey *et al.*, 1989); (ii) they may change position within retreat sites (Schall, 1977). In fact, reptiles may be able to control Tb more precisely inside retreat sites than outside (DeWitt, 1967) and by moving between the surface and a depth of 20cm (Porter *et al.*, 1973; Huey *et al.*, 1989) they may achieve or maintain eccritic temperatures over a large part of each day (DeWitt, 1967; Huey, 1982).

2.3 BIOLOGICAL THERMAL EXCHANGE MECHANISMS

2.3.1 Body temperature gradient

Generally, the body core (abdomen and thorax) is the main centre of metabolic heat production (M) in an animal at rest (Schmidt-Nielsen, 1983) with the skin and muscle mass (body shell) accounting for a lesser amount. Hence, in resting homoiotherms the outer body is generally cooler than the inner body with the resulting temperature gradient (ΔT) providing for passive heat transfer, via blood circulation and conduction, to the body surface and subsequent dissipation into the environment. However, this

situation will often be the reverse in reptiles where these same mechanisms may be used to transport heat to the body core. Heat exchange occurs across highly variable and geometrically complex animal surfaces and it is from these that all heat flux occurs.

2.3.2 Heat-exchangers

Many animals employ countercurrent heat-exchangers in thermoregulation (Schmidt-Nielsen, 1983). These are blood vessels situated in close proximity to each other, and typically arranged in such a way that permits heat exchange to occur between efferent (arterial) blood flow away from the body core and afferent (venous) flow, thus preheating or cooling the blood before it re-enters the core. These systems allow the animals in which they occur to better control heat exchange, even in extreme temperatures. These mechanisms have not as yet been demonstrated to occur in snakes, however as Shine (1991) points out, snakes may preferentially shunt blood through small subcutaneous blood vessels in solar exposed body parts so that the body parts still remaining under cover may be warmed. The flattened necks, typical of basking elapids, accommodate major blood vessels which may be acting in heat-exchange.

2.3.3 Evaporative water loss

Vertebrates typically exhale air saturated with water vapour which may result in considerable loss of water and heat from the respiratory tract. In conditions of heat stress, small vertebrates exploit routes of heat exchange involving a deliberate increase of evaporative water loss (EWL); i.e. through sweating, panting, gular fluttering, licking or urinating on external body parts, or by deliberately seeking out moisture with which to wet their exteriors.

Most reptiles, unlike most amphibians, have integumental barriers to restrict EWL which may allow for activity even in extreme aridity (Gans and Pough, 1982). However, cutaneous water loss can be substantial, though passive, in reptiles (Bartholomew, 1982; Mautz, 1982) The lack of evaporative cooling from the skin means that many small reptiles are prone to overheat as they must depend largely on conduction, convection and radiation as routes of heat exchange. Some reptiles are well known to 'pant' when heat stressed (e.g. geckos), but the amount of water lost by this method may be too small to play a major role in temperature regulation (Schmidt-Nielsen, 1983). Nonetheless, the palate and pharynx of many species are highly vascular with major blood vessels clearly visible just under the epithelium,

including Tiger Snakes *Notechis* spp. and other elapids (pers. obs.), and in many lizards, with obvious potential for heat transfer.

2.4 SUMMARY

This chapter has outlined the terminology of thermoregulation and the thermal repertoires available to reptiles in particular. It has indicated the dependence reptile activity has on microthermal environments and the biological mechanisms which may be operating in thermoregulatory response. It has also outlined the difficulties involved in interpretation; for example, in accurately defining or determining body temperature and in inferring normal thermoregulatory behaviour. The biological considerations figured highly in selecting an appropriate Tiger Snake monitoring programme and played an important part in the interpretation of results.

3 THEORETICAL CONSIDERATIONS

3.1 ENERGY BALANCE

For an animal to maintain a constant body temperature (i.e. be in a steady state with the environment), heat must be lost from the body at the same rate it is absorbed from the environment and is produced through metabolic processes. The general energy balance between environmental variables and a terrestrial animal is illustrated by a simple equation (following Oke, 1978) in the form:

$$Q_a + M = Q_H + Q_E + Q_G + \Delta Qs \qquad 1.$$

where:

Q_a net total radiation absorbed
M metabolic heat gain
Q_H sensible heat flux
Q_E latent heat flux
Q_G ground heat flux
ΔQs net change in body heat store

All the terms in Equation 1. are spatially averaged for the entire animal surface area and expressed as fluxes (Wm^{-2}). For a terrestrial animal with a higher Tb than the environmental temperature the equation may be rearranged in the form:

$$\Delta Qs = M + Q_a - Q_H - Q_E - Q_G \qquad 2.$$

When environmental temperature equals body heat store there can be no net loss or gain of heat. If environmental temperature exceeds body temperature, ΔQs must increase unless balanced by Q_a, Q_H, Q_E and Q_G. However, in the latter situation Q_a, Q_H and Q_G are positive and, as CT_{max} is approached, Q_E becomes increasingly important in balancing ΔQs. Therefore, for ΔQs to remain at constant levels, Q_E must account for all heat gain and increase with increasing temperature. However, there is usually a limit to the amount of water available for Q_E, an amount which varies depending on the species and the habitat.

Generally, for a terrestrial vertebrate in a cooler environment to increase ΔQs it must

maximise M and Q_a and reduce Q_H, Q_G and Q_E. M is limited in most reptiles; hence, when colder than the environment, they may maximise Q_a by means of postural adjustments to maximise solar exposure (heliothermy), or they may select warm substrates and gain heat through conduction (thigmothermy). They may also manipulate their surfaces to adjust albedo and/or increase solar exposure by dorso-ventrally flattening their bodies. These adjustments are reversed when VT_{max} is reached and the animal may then adopt a 'shuttling' heliotherm mode of thermoregulation. Reptiles may be able to further maximise the rate of heat gain and minimise the rate of heat loss by adjustments to heart rate (increased for the warm-up phase) and peripheral circulation (also increased during the warm-up phase).

3.1.1 Radiation

Radiation is exchanged at the animal's surface in the forms of direct sunlight, scattered skylight, reflected sunlight, and thermal radiation emittance from the sky, habitat and animal surfaces. Approximately 99% of incident solar energy is contained within the wavelength range 0.25-4.0 μm (Iqbal, 1983). Near-infrared wavelengths (0.75-4 μm) comprise approximately 46% of the available thermal energy and are largely absorbed by terrestrial animals (Gates, 1980). Animal surfaces generally are highly absorptive to radiant energy in the middle to far-infrared wavelengths (5-25 μm) (Schmidt-Nielsen, 1983). In the far-infrared most hydrocarbon surfaces approximate 'blackbodies' with animal surfaces reflecting less than 5% of energy available, hence, they also have high emissivities (≥95%) at this range (Gates, 1980). The absorptance or emittance of longwave radiation is independent of the degree to which visible radiation is being absorbed or reflected; i.e. animal coat or skin colour does not influence absorptance or emittance in mid to far-infrared wavelengths. However, surface pigmentation determines the amount of shortwave radiation absorbed in the visible waveband, which is an important source of solar energy (approximately 45% of available solar energy), and near-infrared absorptance. Norris (1967) noted that the ability of some reptiles to change skin colour seldom followed variation of the ultraviolet or infrared spectral ranges, however, skin colour change can be induced by changing air temperature. Porter (1967) concluded from his work on the thermoregulatory and ultraviolet significance of black peritoneums in some lizards, that while the pigmented membrane appears to be insignificant in thermoregulation, it is important for preventing entry of significant amounts of ultraviolet radiation into the peritoneal cavity

3.1.2 Radiant flux

Thermal radiant transfer between an animal and any radiating surface occurs at a rate specified by the Stephan-Bolztmann law; for a blackbody this is in the form:

$$R = \sigma(T_s + 273.16)^4 \qquad 3.$$

where:

R radiant emittance

σ Stephan-Bolztmann's proportionality constant $= 5.673 * 10^{-8}$ W m^{-2} °K^{-4}

T_s surface temperature

Most objects do not behave as blackbodies and are said to be greybodies because they have a radiant emittance less than that of a blackbody; their radiant emittance is given by:

$$R = \varepsilon\sigma(T_s + 273.16)^4 \qquad 4.$$

where:

ε emissivity of the surface

ε is defined as:

$$\varepsilon = \frac{L\uparrow - L\downarrow}{\sigma T_s^4 - L\downarrow} \qquad 5.$$

where:

$L\downarrow$ downwelling longwave radiant flux

$L\uparrow$ upwelling longwave radiant flux

Net radiant emittance (R *) between two surfaces may be given as:

$$R^* = \sigma\, \varepsilon_1\varepsilon_2(T_2^4 - T_1^4)A \qquad 6.$$

where:

ε_1, ε_2 emissivities of the two surfaces

T_1, T_2 temperatures of the two surfaces

A effective radiating area

Equation 6. is a useful simplification which assumes that one or both surfaces have emissivities close to unity and may be used with reasonable accuracy only if the temperature difference between the surfaces is less than 10°C (Gates, 1980).

When dealing with radiant energy flux on an animal surface, it is useful for the sake of simplification to consider the animal as a uniform geometric shape. If a rectangular shape is assumed, for a snake, for example, then the net radiant flux on the dorsal surface (Q_{ad}) may be calculated from:

$$Q_{ad} = K\downarrow + L\downarrow - K\downarrow\alpha s - \sigma(T_s + 273.16)^4 \qquad 7.$$

where:

$K\downarrow$ down-welling global radiation

αs albedo of the snake surface ($K\uparrow/K\downarrow$)

T_s snakes's surface temperature

and the net radiant flux on lateral surfaces (Q_{al}) may be calculated from:

$$Q_{al} = 0.5K\downarrow\alpha r + 0.5D + 0.5L\downarrow + 0.5\sigma(T_r + 273.16)^4 - \sigma(T_s + 273.16)^4 \qquad 8.$$

where:

0.5 is an assumed sky-view factor

D diffuse sky radiation

αr albedo of the ground surface

T_r ground surface temperature

Diffuse sky radiation may be defined as:

$$D = K\downarrow - I\cos Z \qquad 9.$$

where:

I direct solar radiation

Z zenith angle of the sun

The net radiant flux density on a snake at ground-level would then be the sum of Equations 7 and 8; assuming the ventral surface is in contact with the ground along its entire length.

3.1.3 Conduction

Increased temperature gradient between body core and shell, or animal and habitat

surfaces, will result in increased thermal conduction; as will decreased distance between the different temperatures. Conductive heat transfer from the body core to the animal surface may be illustrated in a simple form by considering the net heat production (M - Q_E) passing through an insulating layer (In), where the rate of heat flow is inversely proportional to the quality of insulation (K = 1/In) and directly proportional to the temperature difference (Tb - T_s); in the form:

$$M - Q_E = K(Tb - T_s) \qquad 10.$$

where:

K	overall thermal conductance of the body tissues
Tb	deep body temperature
T_s	body surface temperature

Overall thermal conductance (K) of the body shell can be accurately determined if the deep body and surface temperatures, and thermal conductivities between these points, are known. By ignoring M - Q_E, K is defined as:

$$K = kA \frac{T_2 - T_1}{d} \qquad 11.$$

where:

k	thermal conductivity
A	surface area
$T_2 - T_1$	core minus surface temperatures
d	tissue thickness

The combined thermal conductances of a snake in contact with the ground surface and open air is can now be described as:

$$K = k(T_s - Tb) / dd + k(T_r - Tb) / dv \qquad 12.$$

where:

dl	dorsal body wall thickness
dv	ventral body wall thickness

3.1.4 Convection

Increased wind speed ($\bar{u}$) results in accelerated heat transport to or from a surface, and if of sufficient velocity, will take the form of forced convection. The rate of heat transfer by forced convection (hc) between a terrestrial animal's surface and the air is

proportional to the temperature difference. This proportionality constant is the convective coefficient (h) which is a complex function of wind speed, air and surface characteristics. Gates (1975) explains that, assuming a cylindrical shaped animal, the interaction of wind with an animal surface takes the form:

$$hc = h' \frac{\bar{u}^{1/2}}{d^{1/2}} (T_s - T_a) \qquad 13.$$

where:

- h' convective coefficient for a cylinder (3.89 W m^{-1} s^{-1} $°C^{-1}$)
- $\bar{u}$ mean wind speed
- d characteristic dimension
- T_a air temperature

The animal may modify its rate of convective heat exchange behaviourally by changing its posture or shape; e.g. by coiling, flattening or by simply seeking shelter from the wind.

A terrestrial snake living on the ground surface, and within the surface boundary layer, may be protected from the effects of forced convection and free convective heat transfer may predominate. As free convection is assumed for the purpose of modelling the snake's energy budget it is dealt with in section 3.3.3.

3.1.5 Evaporation

Relative humidity (RH) influences the amount of heat lost through the latent heat of vaporization (λ) and is a function of the temperature at which vaporization occurs. The rate of evaporation (E) is directly proportional to the vapour density difference between the site of vaporization and the free air outside of the animal's boundary layer, and is thus a function of animal surface temperature (T_s), air temperature (T_a), RH, boundary and cutaneous resistances to water vapour (r_b and r_c respectively).

If solute concentration at the animal's surface is ignored then λE may be described by the functional notation:

$$\lambda E = f(T_s, T_a, RH, r_b, r_c) \qquad 14.$$

The quantitative value of latent heat is known and varies with temperature; e.g. for an animal at 20°C the heat loss to evaporation is 2.45 * 10^6 J kg^{-1}, and at 30°C it is 2.43

* 10^6 J kg^{-1} (Oke, 1978). In endotherms at moderate temperature this loss may be equivalent to only a few percent of total metabolic heat production. However, it represents a much larger percentage of metabolic heat production in ectotherms.

If the air is very dry, then a steep vapour pressure gradient may exist across the boundary layer; a situation which is reversed in very humid conditions. The rate of water loss is given as:

$$E = \frac{d_s(T_s) - d_a(T_a)}{r_b + r_c} \qquad 15.$$

where:
$d_s(T_s)$ vapour density of saturated air at the animal surface (kg m^{-3})
$d_a(T_a)$ vapour density of free air outside of the animal boundary layer (kg m^{-3})

Therefore, E will decrease with increasing RH at constant T_a, and increase with increasing T_a at constant RH; and if both RH and T_a are held constant then EWL will increase with increasing T_s.

3.2 BIOPHYSICAL MODELLING

> *"The complexities of heat exchange between an animal and its environment have caused some animal ecologists to use oversimplified approaches to the subject (e.g., a Newton's law formulation). A theoretical model of heat transfer between an animal and its environment is not only absolutely essential in the interest of coherent insight into many animal ecology problems, but is also necessary to define the methods of measurement".*
>
> Gates, 1975 (p. 251)

Hall and Day (1977) define a model as an abstraction or simplification of a system; Jeffers (1982) defines a model as a "... formal expression of the relationship between defined entities in physical or mathematical terms". The sheer complexity of natural systems analysis forces over-simplification when attempting evaluation. A model is a compromise between abstraction and the 'real' world. Thus, when developing an ecological model to define any natural process it is important that a balance be found which will provide sufficient detail for validity and predictive precision, yet remain simple enough to allow for a clear understanding of the processes involved (Bakken and Gates, 1975). Hence, theoretical modelling might be considered a contradiction

in terms and can only be expected to provide a view of the 'real' world through a series of successive approximations.

Early biophysical models were used to predict equilibrium body temperatures for reptiles under particular environmental conditions (Norris, 1967; Bartlett and Gates, 1967); or the thermoregulatory effects of colour or posture (Norris, 1967; Muth, 1977). Biophysical models are used in determining the behavioural implications of energy exchange and for predicting the activity patterns of both predators and prey (James and Porter, 1979; Porter and James, 1979). Christian *et al.* (1983) used biophysical modelling to demonstrate that seasonal and weekly adjustments to home range by the Galapagos land iguana, *Conolophus pallidus*, occurred in response to a changing thermal environment. Crawford *et al.* (1983) used multiple regression analyses (using wind speed, radiation load, ground surface and air temperatures) to calculate an operative temperature (T_e) which allowed for accurate prediction of basking behaviour in a terrapin (*Pseudemys scripta*). Temperature is an important ecological resource for which ectotherms will compete (Magnuson *et al.*, 1979; Roughgarden *et al.*, 1981), and, as such, biophysical modelling should allow prediction of activity periods and habitat usage in these species (Spotila and Standora, 1985).

3.2.1 Integrated parameter modelling

Integrated, or 'lumped', parameter models often combine all sources and sinks of energy by assuming the animal to be a simple cylinder or other simple geometric volume.

Net heat production in an animal is M - Q_E and for a general energy budget to be accurate it must account for In. As conducted body heat is inversely proportional to In and directly proportional to the temperature difference Tb - T_s, the energy balance for an animal may be given in terms of its Tb in a similar form as that proposed by Gates (1980) for the steady state scenario. In a small to medium size reptile peripheral insulation is limited, thus the insulative term can be ignored and the energy balance expressed as:

$$M - Q_E + Q_a - \varepsilon\sigma(T_s + 273.16)^4 - hc(T_a - T_s) - Q_G = 0 \qquad 16.$$

where:

Q_a total amount of radiation absorbed by the animal

hc convective heat flux

Q_G substrate conductive heat flux = K(Tb - T_r), where T_r is ground surface temperature

Although an integrated parameter model such as this is inherently simplistic and general in detail, it provides a way to reasonably approximate a reptile's energy budget. This is especially true for snakes which have geometrically simple forms.

The electrical analog shown in Figure 3.1. illustrates the energy flow through an animal without plumage or pelage (following Bakken and Gates, 1975). According to Kirchoff's law net heat flow at any point in the circuit must equal zero:

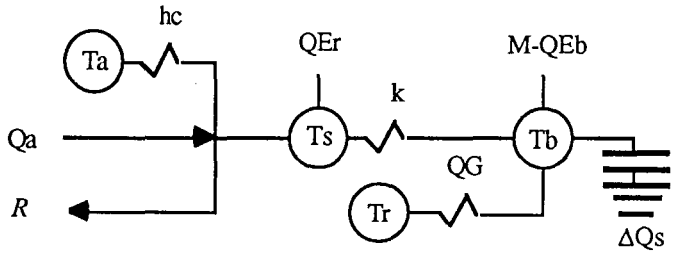


Figure 3.1. Electrical analog of the heat flow in an animal without pelage or plumage

where:

ΔQs	net change to body heat store
Ts	body surface temperature
Tr	ground surface temperature
k	thermal conductivity through the body
hc	convection heat transfer
R	radiant emittance
QG	conductive heat flux to the substrate
QEr	evaporative energy loss from the respiratory surface
QEb	evaporative energy loss from the exterior surface
M	metabolic heat production

Time-dependent analyses of energy exchange mechanisms are necessary to evaluate animals in transient stages of energy flux (Gates 1975, 1980). Hence, for the purposes of defining mechanical heat transfer, the body core loses or gains heat from storage ($\Delta Qs d\mathrm{Tb}/dt$) via conduction to the body surface $k(\mathrm{Tb} - T_s)$, and net heat production ($M - Q_{Eb}$) is in the form:

$$M - Q_{Eb} = k(\mathrm{Tb} - T_s) + \Delta Qs d\mathrm{Tb}/dt \qquad 17.$$

where:

*d*Tb	difference in body temperature
dt	difference in time

and to conserve energy at the surface requires:

$$Q_a + k(Tb - T_s) = \varepsilon\sigma(T_s + 273.16)^4 + hc'(T_s - T_a) + Q_{Er} \qquad 18.$$

Therefore, the general integrated isothermal model for a time-dependent energy budget will include Equations 17 and 18 in the form:

$$Q_a + M - Q_{Eb} - \Delta Qs\, dTb/dt = \varepsilon\sigma \left(Tb - \frac{M - Q_{Eb} - \Delta Qs dTb/dt}{k} + 273.16\right)^4$$

$$+ hc\left(Tb - T_a - \frac{M - Q_{Eb} - \Delta Qs dTb/dt}{k}\right) + Q_{Er} \qquad 19.$$

Equation 19. will account for all of the environmental factors affecting the energy status of an animal in any given habitat (Gates, 1980). However, the quantities M, Q_{Eb} (evaporation from the integument) and Q_{Er} (evaporation due to respiration) may be time dependent as they vary with the 'environmental' temperature and will further complicate the solution. The analysis is simplified if a steady-state is assumed, in which case none of the terms used will be time dependent and $\Delta Qs\, dTb/dt = 0$; the energy budget may then take the form of Equation 20. (Porter and Gates, 1969; Morhardt and Gates, 1974; Gates, 1980). If the values for M, Q_{Eb}, Q_{Er}, Tb, k and hc are known, then any value of Q_a will have a corresponding value of T_a to balance the equation in the form:

$$Q_a + M - Q_{Eb} = \varepsilon\sigma\left(T_s - \frac{M - Q_{Eb}}{k} + 273.16\right)^4 + hc\left(Tb - T_a - \frac{M - Q_{Eb}}{k}\right) + Q_{Er} \qquad 20.$$

Hence, Tb's may be predicted from environmental data using energy budget analysis (Eq. 20.) by solving for Tb at different T_a's until a balance is found and therefore define climate. Using virtually the same methods Gates (1980) considers that this procedure may also be used to calculate the Tb's of animals in burrows.

3.2.2 Climate space

The predictability of Q_a and T_a from M, Q_{Eb}, Q_{Er}, k and hc at critical thermal (CT) maximum and minimum limits permits one to define the microclimatic parameters for the animal in a climate-space (Fig.3.2.).

By treating microclimate as an exploitable resource, climate space evaluation for a given species permits identification of its thermal ecological needs. The original concept of climate-space by Porter and Gates (1969) was extended to predicting the behaviour of several reptiles, e.g. Spotila (1972), Porter *et al.* (1973), Tracy (1976) and Scott *et al.* (1982). Originally the climate space represented a four dimensional space made up of the climatic variables: Q_a, T_a, $\bar{u}$ and RH. Of these, three microclimatic parameters may be used to construct a simple three-dimensional space. When plotted Q_a on the abscissa and T_a on the ordinate allow for predictive estimation of the quantities of Q_a, T_a and $\bar{u}$ needed to satisfy the thermoregulatory limits of a given species (Gates, 1975, 1980). An example of a climate space for a hypothetical animal is given in Figure 3.2. To include $\bar{u}$ requires that the steady-state energy budget be solved (Eq. 20.).

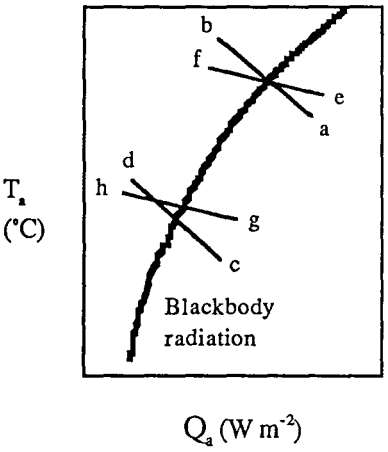


Figure 3.2. Upper and lower thermal limits for an hypothetical animal in climate space. Lines ab and cd are for still air, ef and gh are for a wind speed of 2.0 m s^{-1}. The line lengths represent absorptance and the upper and lower lines the thermal tolerance limits (following Gates, 1980).

Although it is not intended in the current study to determine the climate-space of the Tasmanian Tiger Snake in the above form, as the CT's were not determined, it is intended to determine a modified climate space based on VT's. Further, the method outlined above may not be the most suitable for a terrestrial snake which might minimise its exposure to wind and be more closely associated with inground and ground surface temperatures than with air temperature. In order to develop a complete and predictive climate space model for snake behaviour, however, would require information on CT's and microclimatic parameters for all seasons of the year. The present study is based only on a relatively short summer season, therefore, the complete model cannot here be developed.

3.2.3 Physical models as alternatives

Extrapolating laboratory measurements of metabolism and evaporation to the natural environment is a persistent problem in physiological ecology. To facilitate an understanding of the thermal environment, while avoiding the difficulties associated

with accurate micrometeorological measurement and interpretation, an alternative method has evolved which utilises animal forms as 'environmental thermometers' to derive single-number indices of microclimate. Operative environmental temperature (T_o) (Winslow *et al.*, 1937) and standard operative environmental temperature (T_{es}) (Gagge, 1940; Bakken, 1976) are similar but distinct pseudo-temperatures frequently encountered in the literature when reference is made to the concept of environmental temperature (Bakken *et al.*, 1981; Bakken *et al.*, 1985). Both T_e and T_{es}, as modified for ecological studies (Morhardt and Gates, 1974; Bakken and Gates, 1975; Bakken, 1976; Robinson *et al.*, 1976; Mahoney and King, 1977), respectively, are indices of potential and actual sensible heat flow. They define the combined and highly variable interactions occurring between all environmental variables and the physical characteristics of individual animals. The potential heat flow to and from the animal is Tb - T_e and must be used with a thermal resistance or conductance term. T_{es} is the direct index of heat flow (Bakken, 1981a) and often used specifically to relate the thermal environment to the metabolic requirements of endothermic animals. Both T_e and T_{es} can be calculated from animal or environmental heat exchange parameters (Campbell, 1977; Gates, 1980), or, more simply, may be measured directly by the use of physical models or taxidermic mounts as environmental thermometers which are designed specifically to represent particular species or type (e.g. gender, size class etc.). T_{es} includes accounting for convective heat loss which involves using heated mounts and adjusting T_e accordingly. While detailed energy budget analysis is required to fully define a thermal environment (Porter and Gates, 1969), physical models or mounts provide a simple means of making replicate measurements in confined situations where the use of micrometeorological instrumentation may otherwise be cost-restrictive, physically difficult or impossible (e.g. perches) (Bakken and Gates, 1975, Bakken, 1976; Bakken *et al.*, 1985). Further, such models are useful for comparing the thermal equivalence of different sites (Bakken *et al.*, 1981). Examples where physical models have been used successfully in ecological studies are given in papers by: Bakken and Gates, 1975; Bakken, 1976, 1980, 1981a, 1989; Robinson *et al.*, 1976; Mahoney and King, 1977; Walsberg *et al.*, 1978; Webb, 1980; Bakken *et al.*, 1981; Chappell and Bartholomew, 1981; Roughgarden *et al.*, 1981; Saltzmann, 1982; Walsberg, 1982; Crawford *et al.* 1983; Buttemer, 1985; 1990; Buttemer *et al.*, 1986.

While analysis of microclimatic data is considered adequate for simple habitats (e.g. Porter *et al.*, 1973; Bakken, 1989), in more complex situations physical models may estimate T_e more accurately (e.g. Porter and James, 1979). They may avoid compounding instrument errors and the problem of using over-simplified or inappropriate microclimate models for conditions near the animal. If physical model temperatures are combined with empirical thermal relationships, they can provide test

bodies by which to validate data and to evaluate the relative effects of single parameters (Porter *et al.*, 1973; Bakken *et al.*, 1985; Bakken, 1989).

Mechanistic models (without plumage or pelage) and mounts (covered with original skins and plumage or pelage) may be made from electroformed animal casts, and may be used with or without heated (usually hollow) cores. The choice of T_e and T_{es} (both in W $°C^{-1}$ m^{-2}), and the type of environmental thermometer used, is an arbitrary one depending upon the situation and intended purpose. All cooling may be assumed to act at the core and model body temperature (T_{bm}) represents a nearly instantaneous equilibrium Tb, so that heat storage may be ignored (Bakken, 1980).

T_e is essentially equal to the steady-state temperature a small reptile would attain under stable climatic conditions (Bakken and Gates, 1975; Bakken *et al.*, 1985; Bakken, 1989). For use with reptiles, temperature sensors (thermocouples) are suspended in the centre of the hollow model cavity and respond primarily to the thermal radiation field within (Bakken, 1989). Hence, the data obtained are mean values of the combined wall temperatures within the cavity.

T_e, as defined in the literature, is the temperature of an ideal isothermal blackbody enclosure with the same convective conditions as the general environment, resulting in the same net sensible heat flow from or to the same animal surface or body core (Winslow *et al.* 1937; Bakken and Gates, 1975; Bakken, 1976; Robinson *et al.*, 1976). In ecological studies, body temperature is usually used instead of surface temperature as it is more easily measured. From the above definition, mechanistic models for T_e must be assumed to take full account of wind. Further, it must also be assumed that all heat exchange parameters can be averaged over the entire animal.

Bakken *et al.* (1981) consider that the theory of T_e and T_{es}, as modified for ecological studies, can be illustrated as follows: the animal model has an isothermal core of constant temperature, which may or may not be surrounded by an insulative layer of thermal conductance (K_{sf}), and M and Q_E act at the core. Hence, the heat transfer equations can be reduced to a form similar to Newton's law of cooling:

$$M - Q_E = K_e(Tb - T_e) \qquad 22.$$

where:

K_e overall thermal conductance

T_e operative temperature for the whole animal in the general environment

Following Bakken (1976) K_e between the core and the environment is:

$$K_e = K_{sf}(hc + R) / (K_{sf} + hc + R) \qquad 23.$$

where:

K_{sf} conductance of the animal surface

hc convective heat flux

R equivelent radiation conductance ($4A\ \sigma\varepsilon T_s^3$), where A (m^2 / volume) is the effective radiation area

and T_e can be defined as:

$$T_e \cong (hcT_a + RTs + Q_n) / (hc + R) \qquad 24.$$

where:

Q_n net absorbed solar and thermal radiation

T_e can be measured with an unheated model or taxidermic mount, in which case only the physical animal characteristics (size, shape, colour and pelage) and the environmental conditions will determine the value (Bakken *et al.*, 1981).

T_{es} is defined as the temperature of an isothermal blackbody enclosure with a fixed, standard convective condition which would result in the same net sensible heat flow to or from the same animal with the same surface (Gagge,1940; Bakken, 1976). The choice of a standard convective condition is arbitrary. It can be defined as follows by applying Equation 22 to the definition (Bakken *et al.*, 1981):

$$T_{es} = Tb - (K_e/K_{es})\ (Tb - T_e)$$

$$= Tb - (M - Q_E)/K_{es} \qquad 25.$$

where:

K_{es} is the value in the standard laboratory enclosure of operative temperature T_{es}

It should be noted that because physical models lack circulatory and respiratory systems they cannot be expected to show distribution of heat through the 'body' as would the live animal. Nor is it practical to expect such models to accurately simulate the appropriate physiological (e.g. vasoconstriction or vasodilation, increased or decreased cardiac output) and postural responses without undue complications in design. Simulation of more subtle behavioural and postural responses may not be possible, or even known, and a model may not be able to achieve the intimacy of surface contact as might the live animal. The latter consideration may be especially

relevant to the current study on an animal which habitually has the larger part of its ventral surface in close contact with an irregular ground surface.

3.3 THE INTEGRATED PARAMETER MODEL: ASSUMPTIONS AND DESIGN

The use of accurate microclimatic data in studies of thermoregulation has largely been a neglected area of research amongst biologists; possibly due to the perceived difficulties involved in accurately measuring animal microclimates or in being able to apply such measures at the level of the animal. Nonetheless, the method has the advantage over other physical models in that it uses all of the microclimatic variables to infer the energy status of animals and, when used in combination with appropriate radiotelemetric techniques, may have the advantage in that it uses the actual animal as an environmental 'thermometer'. The combined method uses real Tb values to account for behavioural, structural and physiological adjustments, and may be more flexible than physical models in that it is not limited by predetermined animal position or posture.

This study attempts to estimate snake Tb using an integrated parameter model. The model is developed based on actual Tb response to microclimatic variables and on observed thermoregulatory behaviour.

3.3.1 General assumptions

In dealing with the large number of variables required to model Tiger Snake Tb, it has been necessary to make a number of simplifying assumptions. These include assumptions concerning the snake's anatomy, physiology, posture, incident radiation, radiation balance and convective heat exchange. Wherever possible assumptions were validated through observation or from the field data.

Monteith (1973, p. 156) gives total evaporation rates for reptiles as ranging from 4 to 9mg of water per ml of oxygen consumed, from which he concludes that nearly all metabolic heat production is dissipated by the latent heat of pulmocutaneous evaporation, so that in reptiles $M - \lambda E \approx 0$. Hence, it is assumed that $M = \lambda E$ and that the terms cancel each other and may be dropped from the energy balance equation. Values for K of 0.502 $Wm^{-2}°C^{-1}$ (Porter and Gates, 1969) and for specific heat capacity (Cp) of 3.43 $Jg^{-1}°C^{-1}$ (Bartholomew, 1972) are also assumed for the snake's body. The snake's potential to increase or decrease thermal energy uptake by modifying cardiac output and circulation is ignored at this stage.

In the model, diffuse radiation (D) is assumed to be isotropic, with perfect Lambertian

reflection, and all incident radiation is assumed to be reflected or emitted only once. For emitted longwave radiation both εr and εs are assumed to equal one. For shortwave radiation αs is assumed not to vary as the snake stretches it's skin during the early warm-up phase, and αr is assumed to be uniform within the snake's immediate vicinity. Gates (1980) gives values for dead-skin solar reflectances of three reptile species (an alligator and two lizards) for when the sun is low and high in the sky. The mean albedo values for the three reptile species were: low sun: 0.139, high sun: 0.137. While it is recognised that these values are colour dependent they are initially assumed for αs.

Based on the intimacy of Tiger Snakes with the inground and ground surfaces, Tb's at emergence are assumed to equal T_g at five centimetre depth within night-time retreats. This assumption was validated through measurement of Tb in free-living snakes.

3.3.2 Model design

Q_G and convective effects at the level of the snake were complicated parameters to evaluate, especially as Tiger Snakes have the ability to increase their exposed surface areas. For simplification, the snakes are treated as flat slabs rather than cylinders, while basking, based on the common elapid habit of flattening bodies during early basking periods. This is valid as a large part of the ventral surface area of this species is often in direct contact with the ground surface and is therefore approximately flat. This assumption simplifies estimation of snake surface areas and facilitates the analysis of radiant flux form the snake's dorsal and lateral surfaces. It also simplifies the analysis of convective heat exchange and ground heat flux. The analysis of convective heat exchange was further simplified by assuming that Tiger Snakes minimise exposure to wind during basking periods by remaining under the roughness height of surrounding vegetation, and that free, not forced convection, resulted from their microhabitat selection. This assumption was later validated through wind speed measures over basking pads at snake height.

For the purpose of modelling radiative and convective heat exchange in snakes, snake bodies were divided into four non-equal parts: the neck, fore-body, hind-body and rear. The tail was assumed to play no part in thermoregulation and was excluded from the calculations. The head was included as part of the neck and assumed to have the same dimensions.

The body dimensions were assumed to remain in relative proportion for all size

classes, and each section was assumed to have the same surface area on the ventral and dorsal surfaces. Mean external body dimensions were estimated from actual measurements on live basking animals. The animals used for this purpose included animals smaller and larger than those used for body temperature telemetry. The measurements where taken from the middle of each body section and the body dimensions where then calculated for a standard one metre snout-vent length (SVL) snake. The dimensions for the standard animal are given in Table 3.1:

Table 3.1. Mean live body dimensions assumed by the model for a standardised one metre long unfed Tiger Snake in extreme basking and non-basking postures

	LENGTH (m)	WIDTH (m)	HEIGHT (m)
BASKING			
HEAD/NECK	0.130	0.045	0.005
FORE-BODY	0.310	0.050	0.015
HIND-BODY	0.310	0.050	0.015
REAR	0.250	0.035	0.010
NON-BASKING			
HEAD/NECK	0.130	0.030	0.013
FORE-BODY	0.310	0.035	0.022
HIND-BODY	0.310	0.035	0.022
REAR	0.250	0.025	0.015

The model requires knowledge of mean internal body wall thicknesses. These were determined through dissection of road-killed animals and calculated for the standard one metre SVL snake. These dimensions were: dorsal body wall = 0.0099m (sd=0.0013, n=6); posterior stomach wall = 0.0006m (sd=0.0001, n=6); ventral body wall = 0.0011m (sd=0.0001, n=6). These measures were taken in flat postures and are assumed not to change with the posture of the basking animal. The model assumes that conductivity values are the same for all body structures, therefore the skin and internal body tissues are here considered collectively to form the body walls. Thus the dorsal wall is considered to be 0.0105m thick and the ventral wall 0.0017m thick in the standard animal.

The model assumes the snake's basking posture is to have the body extended or loosely looped with the head and cloaca pointed toward the sun. This posture is occasionally seen in Tiger Snakes and is considered to be a reasonable assumption as these snakes will often lay extended or loosely looped during early basking phase. The model is used to calculate the rate at which Tb is increased following emergence, therefore, it assumes maximum surface area exposure and that dorsal surfaces will be

positioned normal to the sun. These assumptions were later validated through the observation that Tiger Snakes will often use ground-cover vegetation (e.g. grass tussocks) to achieve this position.

The model is presented as a simplified flow diagram in Figure 3.3 and is detailed in the form of a computer programme in Appendix 5.

3.3.3 Convective heat flux

Estimation of convective flux for free convection requires evaluation of Grashof (Gr) and Nusselt (Nu) numbers and the empirical relationships of Monteith (Table A.5a p.224, 1973). Gr is physically described as the ratio of the buoyancy force times the inertial force to the square of the viscous force of a fluid (Monteith, 1973). The model assumes a viscous force (kinematic viscosity) of $1.5 * 10^{-5} m^2 s^{-1}$, which is the value for air at 20°C at sea-level. Gr is given as:

$$Gr = agd^3(T_s - T_a)/v^2 \qquad 26.$$

where:

- a coefficient of the thermal expansion of a fluid (1/273 for a perfect gas)
- g gravitational acceleration ($9.81 ms^{-1}$)
- d characteristic dimension (slab length)
- v kinematic viscosity

Nu is proportional to the ratio of the coefficient of heat transfer by convection to that by conduction in the same fluid at rest and is a function of Gr in the form:

$$Nu = \beta Gr^{\omega} \qquad 27.$$

where:

β and ω are empirical constants

note that Nu is also a function of the Prandtl number (Pr), but as Pr varies independent of T_a this term was not used.

During the field study, Tiger Snakes were invariably found to bask at sites having wind speeds of $\leq 0.5 ms^{-1}$ at a height of two centimetres. The values for Gr were thus determined to be $<10^5$ for these conditions. Hence, the model assumes empirical values for Nu (Monteith, 1973) of:

$$Nu = 0.5\ Gr^{0.25} \qquad 28.$$

Q_H may now be calculated, assuming the value for thermal conductivity of air at 20-30°C, from:

$$Q_H = Nu\ k_a\ (T_s - T_a)/d \qquad 29.$$

where:

k_a thermal conductivity of free air ($2.6 * 10^{-2} Wm^{-1}°C^{-1}$)

The energy budget is solved using Q_H, the net radiative flux on the dorsal (Q_{ad}) (Eq.7.) and lateral (Q_{al}) (Eq.8) surfaces; in combination with specific heat capacity (Cp) and overall thermal conductance (K) of the snake body.

The rate of heat transfer due to conduction (Q_C) to the ground surface is given as:

$$Q_C = K_{c\ mod}\ (T_g - Tb) \qquad 30.$$

where:

$K_{c\ mod}$ overall thermal conductance assumed ($0.502\ W\ m^{-2}\ °C^{-1}$) (Porter and Gates, 1969)

The heat flux on each of the four body parts is calculated from:

$$S = Q_{al}(2VA) + Q_{ad}DA - Q_H(DA+2VA) \qquad 31.$$

where:

S heat flux on each body part ($W\ m^{-2}$)

VA lateral surface area (m^2)

DA dorsal surface area (m^2)

The net heat flux then becomes:

$$ST = (S1 + S2 + S3 + S4) * [(K_{c\ mod} / dv)\ (T_r - Tb)] \qquad 32.$$

where:

ST net heat flux (Js^{-1})

dv ventral body wall thickness (m)

The value for Tb can now be calculated for each ten second period from:

$$Tb = Tb + (10\ ST) / (Ms\ Cp_{mod}) \qquad 33.$$

where:

Ms snake mass (g)

Cp_{mod} specific heat assumed by the model ($3.435\ Jg^{-1}°C^{-1}$), Bartholomew (1972)

and $T_s = Tb$.

The model interpretes the environmental variables each loop and outputs are in ten second time-step changes in estimated Tb and T_s.(Fig.3.4).

3.4 SUMMARY

This chapter has outlined the theory of animal energy balance and the mechanisms of energy transfer between animals and their environments. In so doing it has introduced the sources and sinks of thermal energy available to the animal including: metabolism, radiation, convection, conduction, and the latent heat of evaporation. It has also introduced the biophysical modelling techniques available, including: integrated parameter modelling, climate space theory and physical (mechanical) modelling. The final section gave the reasons which lead to the choice of the integrated parameter/telemetry combined method. It has listed the necessary assumptions and described the model design to be used in determining the thermal status Tiger Snakes. This will be used for predicting Tiger Snake activity based on microclimate.

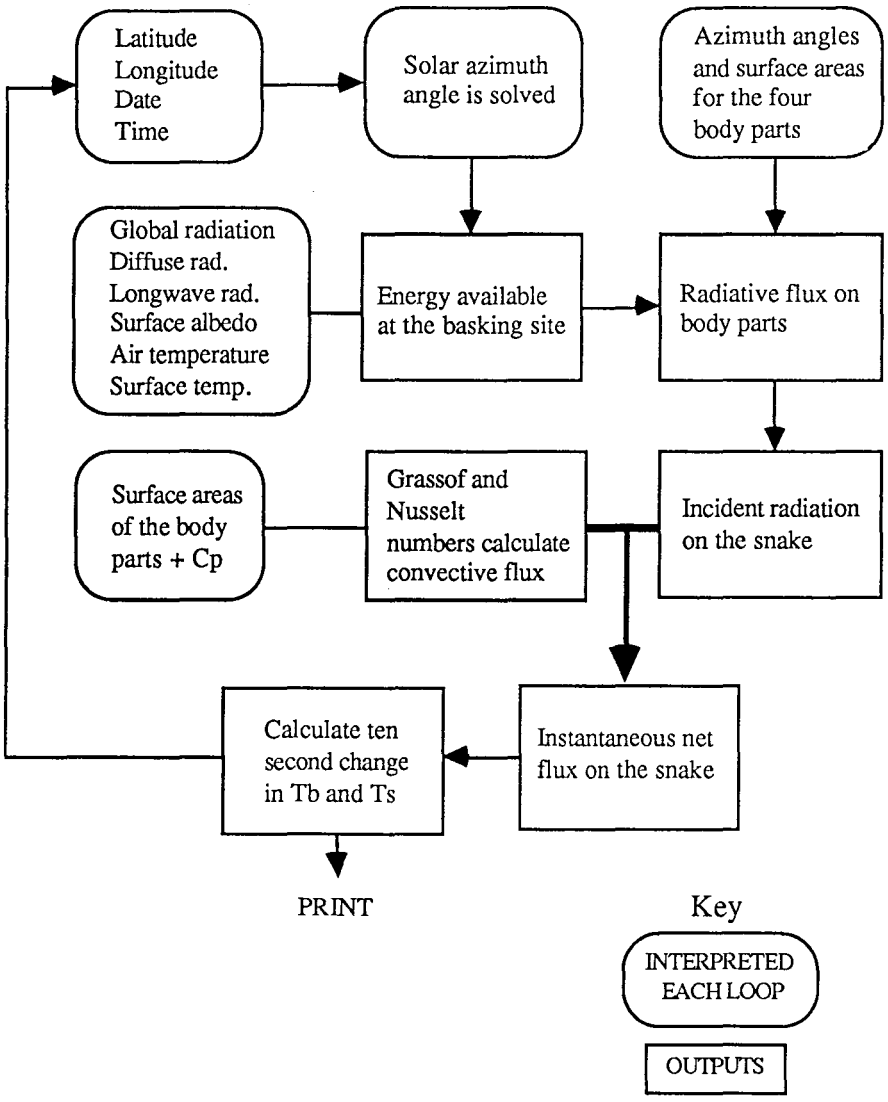


Fig. 3.4. A schematic representation of the procedure used to calculate Tiger Snake body temperature (Tb) and surface temperature (Ts) using an integrated parameter model and computer programme

4 REGIONAL SETTING, SITE SELECTION AND DESCRIPTION

4.1 REGIONAL SETTING

Tasmania is an island comprising approximately 67000km^2 which is situated between the latitudes 40° and 44° South and longitudes 144° and 149° East. The island is located directly south of southeastern continental Australia. Topography is rugged with much of the island elevated to form numerous mountain ranges in the northwest, west, southwest, south and northeast. The most extensive lowland areas occur in the central north, midlands and southeast (Fig.4.1).

A large Central Plateau forms a distinct topographical feature, approximately located in the centre of the island, which is generally well defined by an escarpment and covers an area of more than 10000km^2. It has an average elevation of a little over 600m in the south to approximately 1100m on its northern boundary with glaciated landforms typical in the west and gently undulating terrain characteristic of the east (Pemberton, 1986). The Plateau area contains literally hundreds of freshwater lakes, interspaced with marshes and streams that tend to drain southeast into the Derwent basin.

4.1.1 Climate

The island's climate is generally under the influence of Southern Ocean westerly winds and may be described as cool temperate maritime. As a consequence of the island's topography, the predominant westerlies result in a marked west to east annual rainfall gradient with rain-shadow effects in the midlands and southeast. Mean annual rainfall may vary from more than 2500mm in the West Coast Ranges to less than 500mm in the Midlands. A lee-trough effect is evident over much of the eastern half of the island and tends to channel wind from the north and northwest. The wind regime is further influenced by strong sea-breezes during summer and katabatic winds during winter. The highest mean wind speeds are recorded from the vernal equinox in September through to mid-summer (Langford, 1965). The mean coolest month of the year is July and the mean warmest month is February. The Central Plateau experiences the coolest temperatures with frosts possible in any month above 600m. Snow may fall in all seasons above 1100m, but most frequently from June to September (Ogden and Powell, 1979).

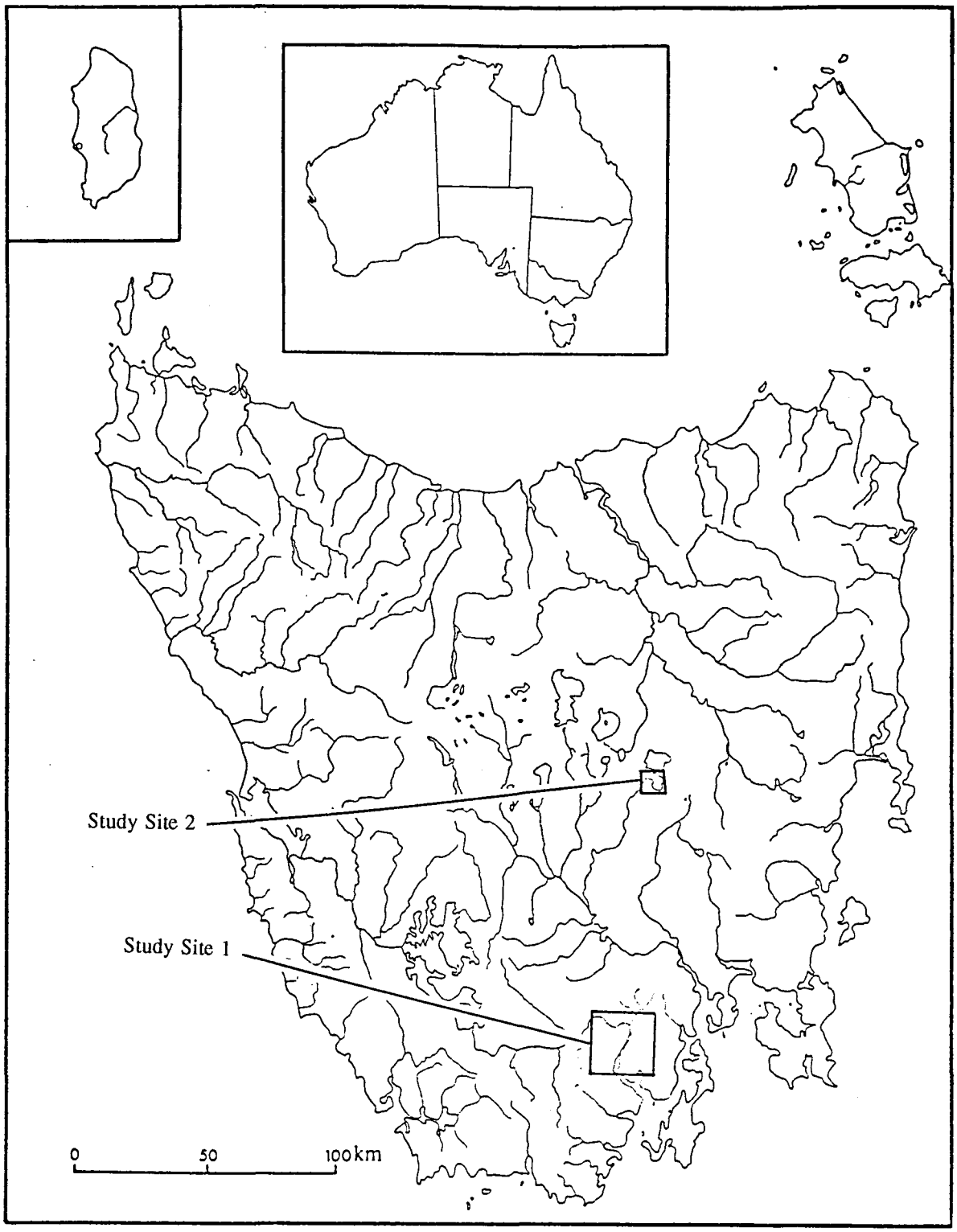


Fig.4.1 Tasmania in relation to mainland Australia, study sites (1 & 2) indicated.

4.2 SITE SELECTION: SURVEY AND CRITERIA

It was realised early in the study that the limited time available for field work would not allow for the finding and monitoring of a large number of animals. Tiger Snakes within reasonable travelling time of the University, situated as it is in close proximity to a densely populated urban centre, are generally scarce and widely distributed. Hence, only limited time was available to travel to, find, mark and monitor snake movements in order to establish study sites.

A pre-study survey was conducted during March and April 1991. The survey was targeted at members of the University of Tasmania, Department of Parks, Wildlife and Heritage, conservation groups and forestry workers. In particular, herpetologists, biologists, national park rangers, geographers, geologists, foresters and expert bush walkers were sought and interviewed. For details of the questionnaire used in the survey refer to Appendix 1.

The results of the survey yielded seventeen possible sites within a one hour drive of Hobart. Each of these were field surveyed for population size and suitability during October and November 1991. The criteria adopted for site suitability are listed below together with the reasons:

a) a healthy population, as ill-health might influence thermoregulatory behaviour;
b) a minimum of six adult females within a relatively small area, in order to ensure enough animals for study and so that all could be frequently observed;
c) isolation from human interference, to ensure as far as possible that the study animals would not be killed or removed by collectors;
d) a relatively undisturbed site, so that the results obtained would be pertinent to interpreting normal behaviour;
e) a relatively homogenous site, in order to reduce the number of environmental variables;
f) ease of access, due to the large quantities of equipment required;
g) close proximity to the University, in the event of any unforeseen problems and in order to reduce travelling time;
h) close proximity to medical support, in the event of a bite; and
i) close access to an electrical power source, in order to recharge batteries.

The best site obtained from the survey which satisfied most of the criteria (a,b,c,d,e,h and i) was at Egg Island, situated as it is in the middle of a large river with a relatively large and undisturbed snake population, and situated relatively close to townships on either side.

4.3 THE STUDY SITES

To gain as much perspective of Tiger Snake microhabitats in Tasmania in the limited time available, the field study was conducted on two elevationally isolated snake populations: the main focus of the study being the sea-level population at Egg Island in the Huon valley; and the other site used only for comparative purposes at Lake Crescent (830mASL). In addition, brief observational studies were made in the general Egg Islands area, Huon valley area, Lake St. Clair area (737mASL) and at Clarence Lagoon (1000mASL)

4.3.1 Egg Island Canal

The Egg Islands are formed of alluvial deposits, are approximately 9.8km long, and situated in the Huon River below the township of Hounville, in southeastern Tasmania.

Fig.4.2 Egg Islands in the Huon River Valley, South-east Tasmania,Study site 1 indicated. (Extract from South-East Tasmania, 1:150 000,1973)

The larger of the two Egg Islands is the southern island which is approximately 7.1km long and bisected in its thinnest part by a 370 x 9m canal. The canal is situated -43°05'10" south and 147°01'0" east between the townships of Franklin and Cradoc, at a point where the river is approximately 730m wide. The canal was originally dug by Henry E. Clark in 1884 with a horse-drawn long-handled scoop. When first excavated the canal was 6.0m wide and 0.6m below low-water (R. H. Cato, pers. com.). However, the canal is now approximately 11.0m wide at its widest point and in several places it is in excess of 1.0m below low-water. The Egg Island study site comprised the entire canal area to ten metres inland from each shore (Fig.4.2).

The shores are in the form of levees which were formed when the canal was excavated. Consequently, the levee soils uniformly comprise a dark grey silt which grades into a humic black soil only where levees adjoin nearby marshland. The organic content of the levee soils was determined from six soil samples; taken from the middle of the southern levee (three) and from its border with the marsh (three). These were burned at 450°C for five hours in the laboratory and determined to have mean organic contents of 5.1% and 12.6% respectively. The levees represent the only entirely dry soils on that part of the island and therefore represent a distinct and isolated topographical area. The latter is reflected in wildlife concentrations and in the vegetation, which on the levees is confined to thin strips with the densest stands occurring on the levee/marshland border. The major plant species found at the canal site are listed in Table 4.1.

Table 4.1 Major plant species occurring at the Egg Island Canal site

	SPECIES	SITE TYPE
Monocot species:	*Gahnia trifida*	levee/dry sites
	Juncus sarophorus	marsh
	J. pallidus	levee/dry
	J. krausii	levee banks
	Isolepis nodosa	levee banks/moist
	Carex appressa	levee/dry
	Poa labilliarderi	levee/dry
Dicot species:	*Eucalyptus ovata*	elevated sites
	Pomaderis apetala	dry sites
	Acacia verticillata	levee/marsh border
	A. dealbata	dry sites
	Melaleuca squarrosa	moist sites
Pteridophyte:	*Pteridium esculentum*	levee/dry sites

The island lacks surface rock and has very little fallen timber. As a consequence, cover is afforded the animals largely from the denser ground-level sub-canopies and ground litter. The islands are relatively flat and the levees represent the highest elevations in the immediate islands area with a mean elevation of approximately 1.5m above high water (Fig.4.3).

Fig.4.3 The Egg Island canal site at low tide.

Both sides of the Huon River valley are flanked by hills which obstruct sunlight into the valley in the early morning and late afternoon. The highest peaks relevant to incoming solar radiation at the canal site are: Woodstock Hill to the east (86°) with a height of 327m and an obstructed solar view to 7.5°; Mansfields Hill to the west (270°) with a height of 512m and an obstructed solar view to 8.6°.

The nearest meteorological station is at Grove, 13km NNE (-42.59°S 147.05°E) at 60m elevation. A rainfall station is maintained at Huonville (6.5km, NNE) and also was, until 1991, at Franklin post office. Information was taken from all of the above to infer the local climate. The predominant local winds experienced during the study period were from the southwest and northeast, due at least in part to the north/south orientation of the river valley, and which included night-time katabatic flows and afternoon sea breezes. Mean annual rainfall is approximately 800 to 1000mm (889mm during the years 1989-1990) with the highest mean number of rainfall days occurring

between July and October (Bureau of Meteorology data from Franklin post office). The following information was taken from Bureau of Meteorology unpublished records for Grove. Extreme monthly mean air temperatures are 22.2 and 9.4°C in January and 11.4 and 1.9°C in July (1952-1986); however, temperature values for Grove may not pertain to the study area due to its littoral situation. Snow is a rare occurrence in this part of Tasmania, however, frosts occur an average of 14 days in July and 0.4 days in January (1957-1991). Mean 10cm soil depth temperatures range between: 15-20°C (0900 EST) and 22-29°C (1500 EST) in January, and 4-7°C and 7-9°C respectively in July (1964-1991). Daily mean sunshine hours are 7.7 hours in January and 3.0 hours in June (1960-1991).

South Egg Island has been used for grazing in the past, but at present the only form of disturbance occurs from infrequent visits by fishermen and power and communications maintenance crews. Fires are reported to occur every few years and the last fire was deliberately lit during the summer of 1988/89 (K. Lowe, pers. com.). The relatively high frequency of fire is evident from dense patches of Bracken, *Pteridium esculentum*, (a fire-weed) which cover extensive areas on both levees.

For the purposes of study the Canal site was divided into three sub-sites; designated S1, S2 and S3. Both S1 and S2 are each 50m long and 10m wide and located on the south shore levee, approximately 300m apart; and both represent the most densely populated snake sites in the canal. Individual home-ranges represented further subdivisions of S1 and S2, and the details of the microtopography, vegetation and height are given in Figures 4.4 and 4.5 respectively. Sub-site S3 was located on the north shore levee and was 200m long and 10m wide (Fig.5.1). The latter was a relatively large site and, due to the scarcity of snakes on the north shore levee, was used for comparative purposes only.

4.3.2 Lake Crescent

Lake Crescent is situated on the south-eastern edge of the lower Central Plateau and was initially chosen as a comparative study-site based on the observations of Dredge (1981). It is a natural lake situated on Jurassic dolerite which outcrops extensively around the lake's perimeter. Only the western lake area was used in the study, which included two sub-sites: the south shore of Brownwater Lagoon (approximately one kilometre west from the lake) and Clyde Marsh (on the western shore of Lake Crescent); both located in the approximate area 140° 08' East, -42° 11' South (Fig.4.6). Brownwater Lagoon is a shallow seasonal waterbody, approximately 400m across at its widest extent, which regularly dries up during the late summer months. Clyde

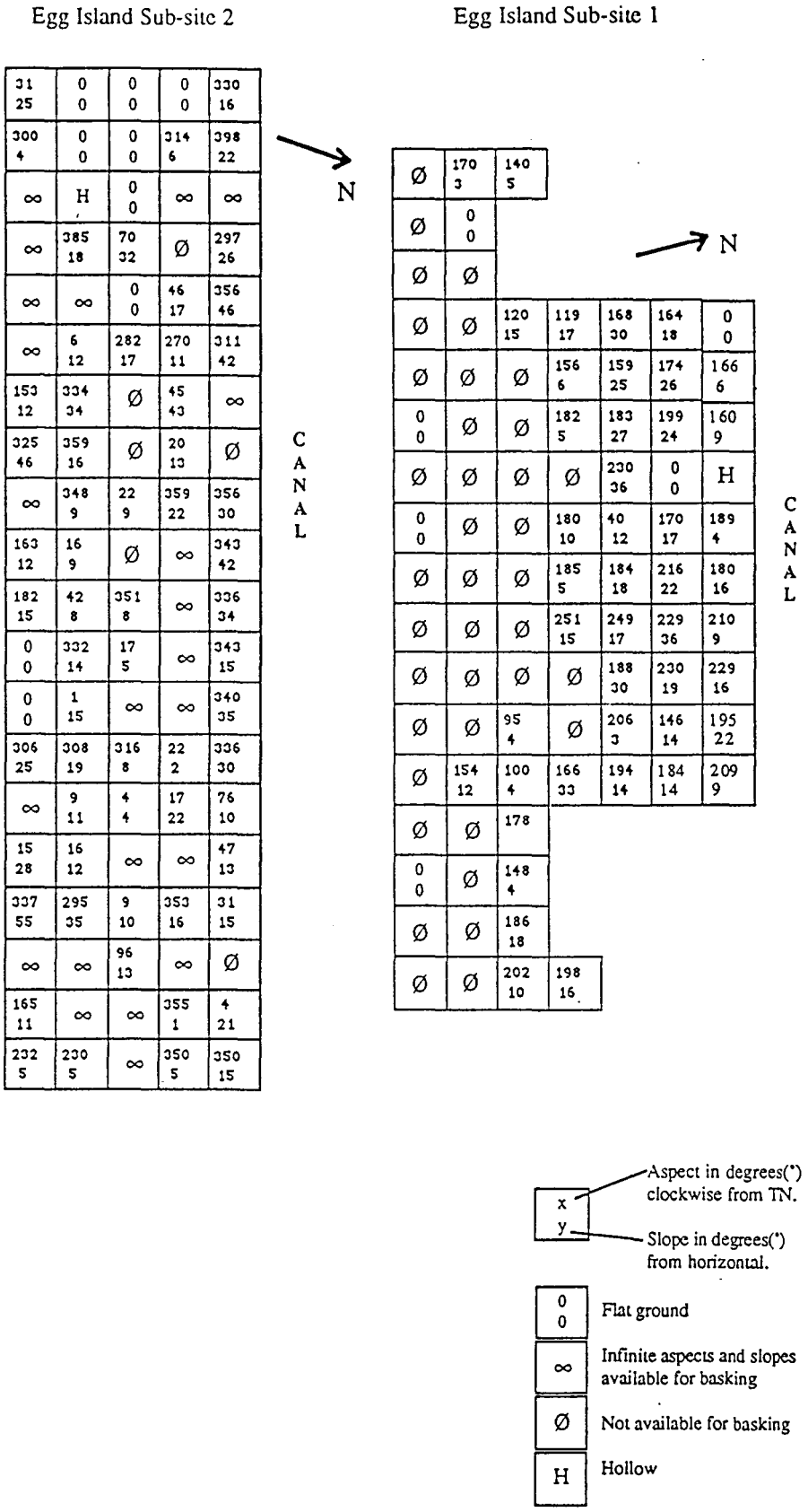


Fig.4.4 Mean slope and aspect of one meter quadrats available for basking for the Egg Island Sub-sites 1 & 2.

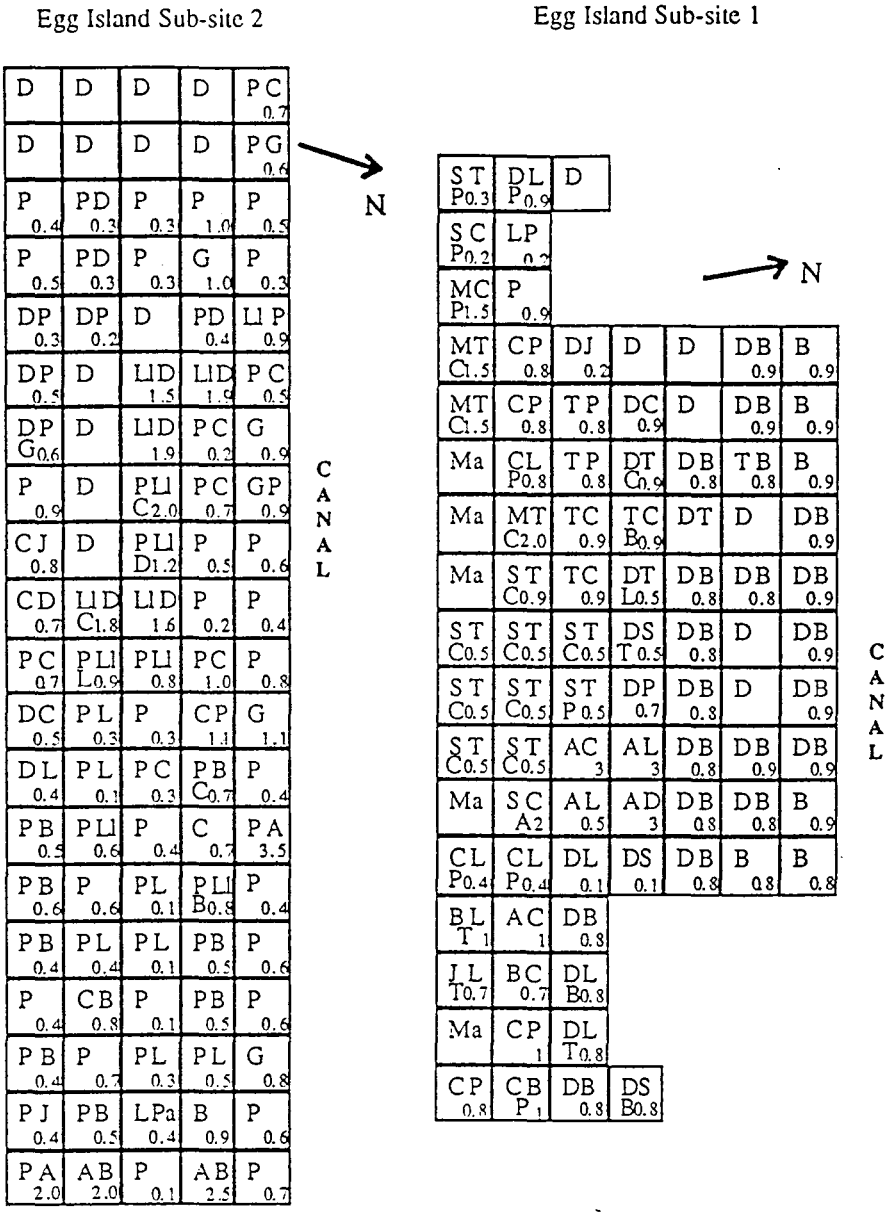


Fig.4.5 Major vegetation types and mean vegetation height of one meter quadrats for the Egg Island Sub-sites 1 & 2..

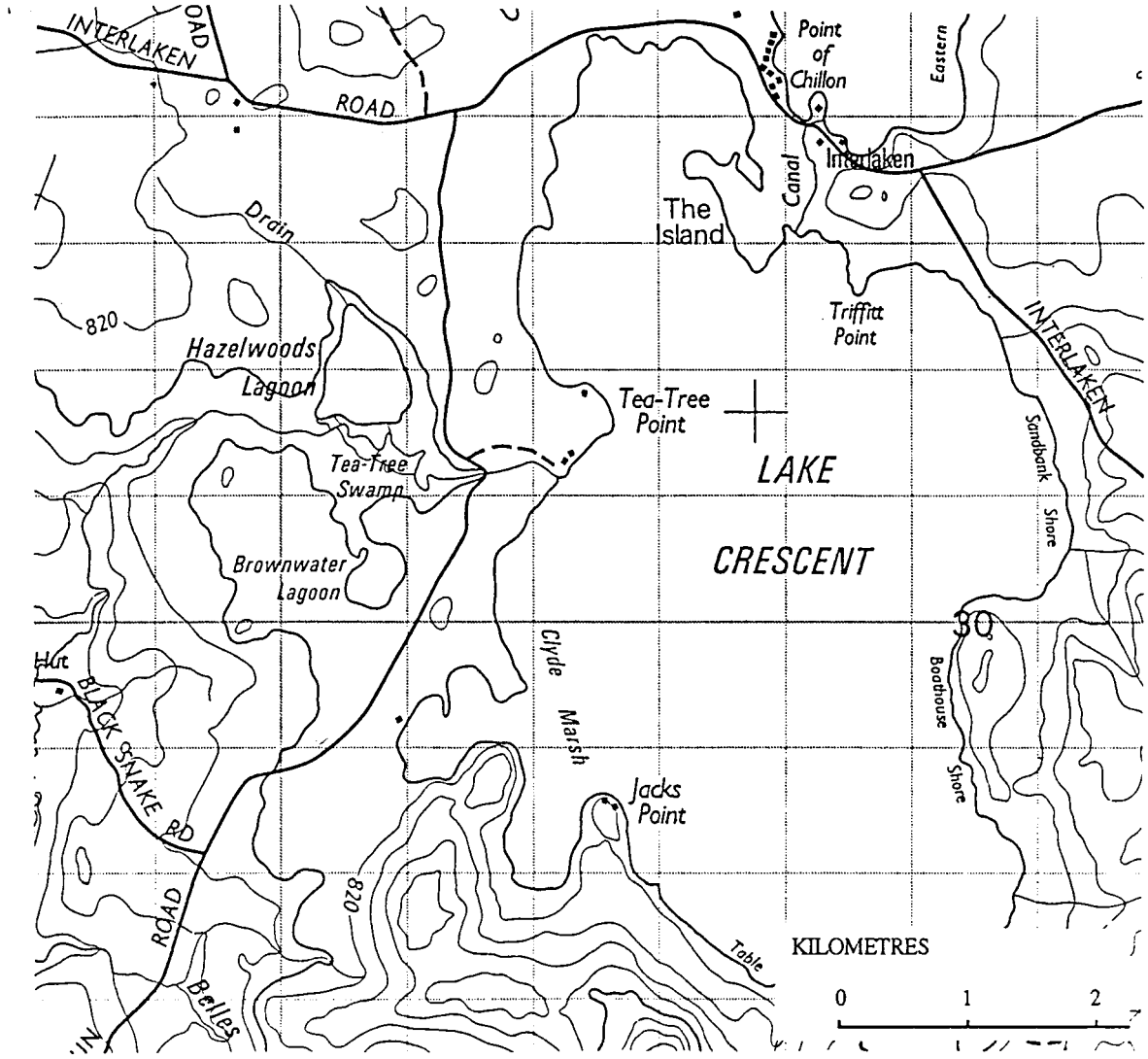


Fig.4.6 The comparative study area of Lake Cresent, South-east Central Plateau.(Extract from Lake Sorell (8313-IV), 1:50 000, 1974.)

Marsh may also become very low, or dry, due to the lake's current use as an irrigation reservoir; which regularly results in a sudden lowering of the water-level. Marshland is common on the western shore of the lake and the local vegetation may generally be described as predominantly *Eucalyptus rodwayi* woodland/*poa spp.* grassland, interspaced with *E. delegatensis* and *E. pauciflora* woodland/grassland/heathland.Climatic records are largely unavailable for the Lake Crescent area and the local climate must be inferred from mean values pertaining to elsewhere on the Plateau. The predominant winds in the general Plateau area are NW to SW and annual mean rainfall is approximately 740mm per annum; with the highest number of rainfall days occurring between August to October (unpublished records from Mt. Serat: -42.13°S 147.06°E, Bureau of Meteorology, 1983-1989). Extreme

mean air temperatures for the plateau area are: 18.4°C maximum and 6.5°C minimum in January; 6.3°C maximum and -0.5°C minimum in July (Pemberton, 1986). Pemberton (1986) gives 1740 hours as the annual mean sunshine hours for Lake St. Clair (western plateau area) and estimates that this value could be as high as 1900 hours in the east (Lake Crescent).

The area is used extensively for grazing of both cattle and sheep which maintain a low ground cover. The area is also regularly subject to firewood cutting/collecting, hunting and fishing activities; all of which have contributed to littering and a common scarring of the landscape from numerous four-wheel drive tracks. In the recent past the Lake Crescent area was well known for its snake populations (Dredge, 1981), however, there has been a sharp reduction in numbers in recent years, possibly due to local hunters and fisherman who admit to regularly killing snakes on sight or actively hunting them. Firewood collecting also results in the removal of potential retreat-sites and may result in increased encounters between man and snake.

5 DATA ACQUISITION

5.1 INTRODUCTION

The methods and techniques used in data acquisition are dealt with in the following in three sections covering: animal measures and monitoring, telemetry techniques and microclimate measurement and monitoring. Animal handling techniques have been included and described in detail as it is felt this is an important aspect of the study; and if done correctly will minimise the danger both to the operator and subject, and ensure as far as possible a valid non-stressed response from the animal.

For the field study no single method would allow estimation of all aspects of thermoregulation (see Biological Considerations, Sections 2.2.6-2.2.8). Indices used to measure thermoregulatory adjustments in reptiles have included shuttling behaviour and percentage of time spent in the sun (Spellerberg, 1972), and the percentage of a population in the sun (e.g. Huey, 1974b). However, these indices alone may lead to misleading conclusions concerning environmental limits to thermoregulation unless they are accompanied with detailed information concerning normal behaviours and microhabitat parameters (Heath, 1964; Huey, 1982); e.g. the amount of time animals are afforded opportunity to thermoregulate in full sun (Huey *et al.*, 1977).

5.1.1 Strategy

In order to reduce the number of variables, related to gender and body mass differences, only adult females were used in the study. The strategy adopted for field studies was as follows:

(i) find a suitable population;
(ii) study normal behaviours;
(iii) mark all adults;
(iv) conduct a trial field study;
(v) monitor Tb of a single female;
(vi) record behavioural thermoregulation in telemetered and control animals;
(vii) monitor microclimatic variables,
(viii) map home-site use;
(ix) determine VT's and mean eccritic body temperatures in the laboratory.

The field studies ran for ten weeks during the summer of 1991/92 (from 21.12.91 to 1.3.92).

The initial trial study of the Egg Island canal site was conducted in the last week of December. The aim was to test the methods of measurement, to study home-site use, determine normal daily activity patterns in females, and to find, measure and identify as many animals in the area as possible. This was followed by a nine week period during which four eight-day, one five-day and two one-day field studies where conducted. These included: four eight-day studies at Egg Island; one five-day and two one-day studies at Lake Crescent. Each eight-day field study at Egg Island required three days for mapping, transporting, setting-up, finding, observing, catching, implanting, releasing and re-catching the telemetered animal, with five days for monitoring the animal and microclimatic variables. In addition to the eight days required for field-work, a further three days were required to determine mean eccritic body temperatures in the laboratory. The initial five-day study at Lake Crescent involved exactly the same procedure as the Egg Island site, except that the study was terminated early due to the sequestering behaviour of these higher altitude animals. Following the initial Lake Crescent study the mean eccritic body temperature was determined. The sequestering behaviour and eccritic Tb's were monitored for four weeks until the snakes became more active.

The following are detailed descriptions of the methods and equipment used in the measurement and monitoring programmes; these are dealt with as: (i) animals, (ii) telemetry, (iii) microclimate.

5.2 ANIMAL MEASUREMENT AND MONITORING PROGRAMMES

The sea-level site at Egg Island was first surveyed and found suitable for study in early November 1991, but the animals in the area were not caught, sexed, measured, marked and released until late December. The animals at the 830mASL Lake Crescent site proved more difficult to find, possibly due to collecting activity in the area the previous year and possibly also due to season. As a consequence of limited time, the low number of active animals and the dispersed nature of the population, the Lake Crescent animals could not be caught and marked prior to commencing the monitoring programmes.

5.2.1 Capture records and sexing

Upon initial capture, and prior to marking, all animals were sexed, measured for total body length, tail length, midbody diameter and weighed. In addition, note was taken of the general condition, scarring and other gross morphological features, time and site of capture.

Sexing was accomplished by gentle probing of the epithelium just under the anal

scale, external and caudolateral to the cloaca, with a small blunt silver lacrimal probe of approximately one millimetre diameter. If this instrument is lubricated with a small amount of soapy water and gently rolled between middle finger and thumb it will pass through into the hemipenes of males easily, requiring very little force, and presents very little risk of damage or discomfort to the animal if the tail is held straight. However, adult females also have a small fold in this area but, while the probe may be easily inserted several centimetres in adult males, probes will not penetrate more than a few millimetres in females. This is the only certain way of sexing Tiger Snakes, when males are not in breeding condition, other than by internal examination or by applying undue force in an effort to evert the organs (either through palpation or injection of an isotonic solution into the mid-ventral base of the tail in animals too small to be probed). Other methods used to sex adult Tiger Snakes in the past have included relative tail lengths and shape (Dredge, 1981), and male aggression (a widely held belief by the Tasmanian public). However, tail measurements made on entire animals during this study showed no noticable difference between the sexes, with tail lengths as a percentage of total body lengths found to be 16.41% (sd=1.362, n=20) in females, and 16.51%(sd=1.552, n=14) in males. Note that animals with tail tips missing were not measured and this is collective data (live and road-killed snakes) taken from several areas within the State, and ranging from different elevations: sea-level to 1 000m. Although Tiger Snakes may give the impression of aggression while in defensive posture, no aggressive animals were encountered, nor were males found to be more noticeably aggressive than females, during the course of this study (early November to early March).

Sexual dimorphism in body size has not been observed to occur in mainland Tasmanian Tiger Snake populations by the writer. However, it has been reported that males are slightly larger than females in areas of N.S.W. and Victoria (Shine,1987a), and Schwaner (1985) found that males grew significantly larger than females on four of the islands he studied, while not on others. At the Egg Island canal site all adult females encountered were noticeably smaller than the males, in animals where sex had been determined; adult female mean SVL was 83.86cm (sd = 2.95, n = 8), male mean SVL was 108.62cm (sd = 12.88, n = 5). The female measures represent the largest animals encountered and which were selected for study based on their size. These sexual differences are not apparent in snake populations just a few hundred metres across either side of the river, at Cradoc or at Franklin, where females of >1.0m SVL are common (pers. obs.). As the canal area is subject to frequent use by small pleasure craft, and as the largest females appear to be concentrated in this area and more closely associated with particular home-sites than males, a pseudo-selection may be occurring in that the larger females are more visible to human visitors and

therefore more frequently killed or collected. Smaller females are often found living on the edges of the more open home-sites and may, therefore, simply take up residence in the absence of a larger animal. Further, males may have become larger through selective pressure imposed by the need to compete for the limited number of suitable sites and the females they contain.

5.2.2 Identification and marking

For the purposes of this study Tiger Snakes were deemed to be adults if they measured ≥0.8m SVL. This is an arbitrary minimum body length parameter based on a 0.81m SVL gravid female specimen donated from Longford Tasmania. The resident population at the Egg Island canal site was initially found to contain thirteen adults: eight females and five males (all males were >90cm SVL), with a smaller undetermined number of subadults. All thirteen animals were identifiable by early January 1992 either from painted tail tips, to indicate capture site, and/or from prominent scars on the body (a number of animals at both field-study sites carry scars, many of which indicate severe injury earlier in life).

In addition to tail paint, animals were clipped on two ventral scales; the first, a square-shaped clip on the tenth ventral scale anterior to the anal scale to identify it as a study animal; and the second, a V-shaped clip anterior to the first and corresponding to the identification number of the animal. Scale clipping was necessary to identify animals after skin-shedding and two clipped ventral scales were found to be necessary due to a high incidence of torn or scarred scales present in the population from natural causes. All scale clipping was undertaken soon after capture and involved first cleaning and wiping the area with a 10% iodine surgical swab (Deseret® Povidone Iodine Swab Stick). On no occasion was noticable bleeding induced by the procedure, as it only required that the scale be clipped to a depth of a few millimetres, or until contact was made with the external ventral body wall. Animals showed only little sign of discomfort during scale clipping, however, as a precaution against it interfering with normal activity patterns, no animal was used for two weeks following the procedure.

5.2.3 Egg Island animal selection criteria, numbers and monitoring

Adult females were selected for telemetry if they seemed to be associated with a particular home-range and retreat-site. This was necessary to ensure the relevant placement of instruments and so that the animals would remain within range of the receiver, at least at night, as a precaution against loss of telemeters in dense cover.

This criteria immediately disqualified two of the smaller adult females, and would also have disqualified all but one male had they been used. Animals were also selected based on body size as it was considered important to minimize the size of the transmitter relative to body mass in order to avoid unduly influencing digestive basking behaviour. The selection criteria for minimum body mass became ≥300g, due to relatively small size of available study animals, which held transmitters to ≤3% of body weight. These criteria limited the choice to five females, four of which were used (A1, C1, A2 and B2). The four selected animals were observed over the entire field study period and recaptured for implantation as needed. A fifth female (A3), although initially selected, was not used as she was later found to move about extensively and use several sites within a 260m area, on both sides of the canal and often in dense cover. Females <300g and/or not closely associated with a discernable home-range were used for observational purposes only.

It was only possible to monitor Tb of a single animal at any one time. All other females within the study area were treated as controls and monitored concurrently with the telemetered animal for behavioural comparison. During monitoring, telemetered and control animals were left as undisturbed as possible and great care was taken to achieve this. Whenever possible, animals were observed from beyond their visual range, through binoculars, as it was intended that monitoring of the animals and their microenvironments should go unnoticed. However, dense ground cover and the snake's relatively poor eyesight often meant that they could be observed from within ten metres without disturbing them.

At Egg Island each telemetered animal's Tb was recorded continuously over a five day period and the position of the animal checked every two hours between 0700 hours and 1900 hours EST, or until the animal re-entered the night-time retreat. In addition, the animal's posture and position were recorded continuously from the time of emergence (from the night-time retreat) to when the animal left the basking-site/sites. The thermoregulatory behaviours of other nontelemetered adult females within the vicinity were also recorded at two hourly intervals if circumstances permitted. Seven of the eight adult females in the population were continuously sought and used for this purpose (six discounting the telemetered animal). These were located at two sub-sites (S1 and S2) approximately 300m apart (four at S1 and three at S2) on the south shore of the canal (Fig.5.1). Animals at a third sub-site (S3) on the north shore were also recorded, but this site was used only infrequently by snakes inhabiting a densely vegetated marsh area. These few animals usually only appeared on the levee in a northerly wind or on very overcast days with little incoming solar energy. Animals at S3 were usually either juveniles or relatively large animals, usually observed only once or twice, and based on the relatively large body size of the latter were considered to be mostly males (see Section 5.2.1).

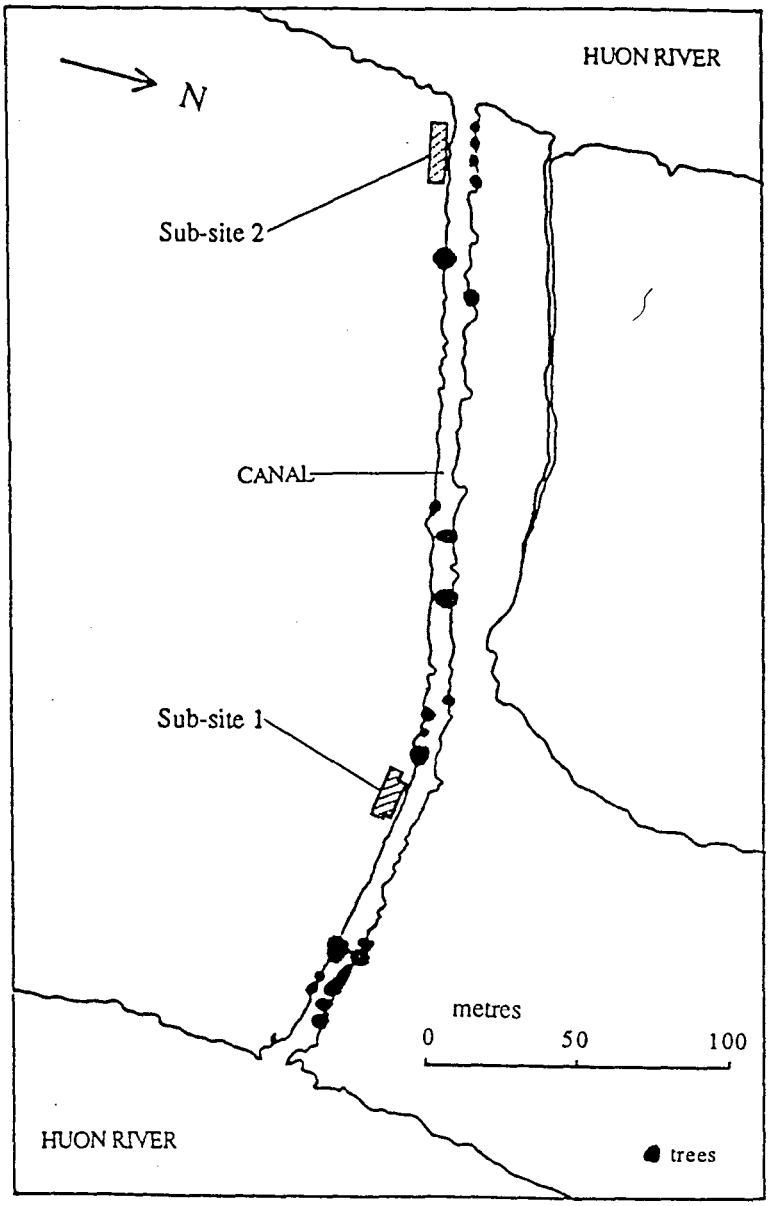


Fig.5.1 Sketch map of the South Egg Island study site showing the location of sub-sites 1 & 2.

5.2.4 Lake Crescent animal selection criteria, numbers and monitoring

The procedure outlined for the Egg Island animals did not apply to animals at the Lake Crescent site. Here the purpose was simply to compare behaviour with the sea-level animals, under known meteorological conditions, regarding the percentage of animals basking, the number of animals active, and the distances travelled between basking and retreat sites.

The method used was to walk the Lake Crescent area in a predetermined pattern for

two hours in the morning (between 0900 and 1100 hours), repeat the same walk at midday (1200 to 1400 hours) and again in the afternoon (1500 to 1700 hours). The number of animals observed, behaviour, location and the microclimatic variables: c, V, $\overline{U}$, $\overline{u}$, Ta and Tr, were measured and recorded.

On three occasions, approximately two weeks apart, a single adult female was captured at Lake Crescent (on the 18.1.92, 6.2.92 and 20.2.92 respectively). Apart from the first which was telemetered and released, these were immediately transported to the University and placed into a temperature gradient in order to determine mean eccritic body temperatures. Selection of animals for this purpose was simply to take the first adult female encountered on each occasion.

5.2.5 Procedure for determining eccritic temperatures

At the end of each field trip animals were transported as soon as was possible to the University in order to determine VT limits and mean eccritic temperatures.

On arrival at the University, a telemeter was implanted if not already in place (all Egg Island snakes still carried telemeters at this stage), and within twelve hours of capture each animal was placed by itself into a temperature gradient chamber for a period of sixty hours. The animal was allowed twenty-four hours to settle down and, following this period, the eccritic Tb was recorded continuously for a further thirty-six hours. A settlement period was found to be necessary as during this time animals exhibited long hours of escape behaviour, evident as numerous spikes of short duration on body temperature charts. The amount of time an animal could be left in the temperature gradient was limited due to the danger of acclimating the animal to the captive conditions and the possibility of influencing thermal response.

The temperature gradient was established in a large wood and glass cage, 2m x 1m x 0.9m, which was lined with brown paper along the floor and walls to ensure the animal could not see out and would remain as undisturbed as possible. In order to minimize influencing the movements of animals within the cage, the cage contained no furnishings except for a low shelf along the back wall (at a height of 3cm and a width of 15cm, to accommodate the secretive nature of the species) and running the length of the cage in the same direction as the temperature gradient. To further avoid influencing behaviour, the heat sources were applied to the outside of the cage and were not visible to the animal as a single point source. Food or water was not included as it may have influenced movement and initiated digestive behaviour. The lack of food or water may be considered nonstressful in a species which habitually

may go without these substances for periods longer than the required sixty hours.

The temperature gradient chamber was housed within a darkened room in the basement of the Zoology Department (Fig.5.2) with an ambient air temperature range of approximately 19-21°C. Heat sources were placed at one end of the cage and included a double-element metal-encased bar heater positioned 20cm under the floor of, and extending the width of, the cage, and two 240W spot lights directed at the corner of the floor and wooden side of the cage. The other end of the cage was air cooled by a fan placed on the floor of the room and directed to force a continuous stream of air from outside the room up onto the side of the cage. This resulted in a temperature gradient within the cage of approximately 21.5 to 39.0°C (±2°C).

Eccritic temperatures were recorded using the field telemetry equipment (Fig.5.2) which is described below.

Fig.5.2 Temperature gradiant chamber in use with field telemetry equiptment. (photo, R.Mawbey)

5.2.6 Stress of handling

The writer was the only person to catch and restrain snakes during this study. Handling by field assistants only involved supporting the caudal-half of the snake's body during periods when the heads were fully immobilised for the purposes of measurement, sexing, marking, implantation and removal of telemeters.

All handling procedures were conducted gently and as quickly as possible, and were undertaken without the use of chemical restraints and without exposing any animal to temperature extremes outside of known physiological limits.

Handling stress was kept to a minimum by limiting maximum handling time per animal to ten minutes; on each of four occasions. These occasions were: (i) capture and restraint for initial examination and marking procedures; (ii) capture and restraint for implantation; (iii) capture for transporting to the temperature gradient; (iv) restraint in order to remove telemeters. Snakes were held and transported in soft calico bags, or were in the temperature gradient; with the exception of two gravid animals (C1 and Cr3) which were housed in a cage after the field work was complete for reasons explained below. Newly captured snakes were sexed, weighed, measured, marked and released at the first opportunity.

5.2.7 Use of captive and road-killed animals

Prior to beginning the field study, four adult Tiger Snakes were housed in captivity: two from sea-level and two from the Lake Crescent area (830mASL). These animals were collected over the eighteen month period prior to commencing the study and were purposely handled frequently until they became tolerant. They were used to develop techniques for nonsurgical implantation and removal of telemeters, to test telemeter function before implantation into free-living animals, and to measure live body dimensions while in various basking postures in order to estimate body thickness and exposed surface areas. For the above reasons, these animals were not over-fed while in captivity; they were fed an average of one dead medium-sized adult mouse every ten days in an effort to keep them as representative of wild animals as possible. Tiger Snakes are prone to over-feed while in captivity and, despite the relatively small number of meals, all managed a 2-6% increase in body weight over the captive period.

In addition to the above animals, use was also made of dead animals (road killed), when available and if not too extensively mutilated, in order to determine: dead skin

reflectances, stomach thickness/body length ratios, body wall thickness/body length ratios, tail length/body length ratios and the relative position of the pyloric sphincter. The latter in order to determine the resting position of a stomach implanted telemeter, in the unfed animal. All donated road-killed animals were males.

5.3 TELEMETRY

5.3.1 Capture and restraint

Capture of adult animals was achieved by the use of bare hands and open-mouthed bags made from lightweight fish landing-net frames and white calico. Capture usually involved a slow stalk directly towards the animal followed by a rapid but gentle grasp of the cloacal region, picking it up and coaxing the animal as soon as possible into a bag. Speed was considered important in order to minimise risk and stress both to the animal and to the handler. Alternatively, if time of emergence from the burrow and the choice of basking pad could be deduced from the micrometeorological conditions, one simply waited in ambush for the snake. Capture of animals to be telemetered was undertaken in late afternoon, in order to minimize time in the bag (held to less than two hours) and to avoid possible temperature stress to the animal. Following implantation, the snake was held in the bag for an hour to calm it and to guard against regurgitation. Release occurred at the entrance to the night-time retreat, after first checking the transmission, at a time when the particular animal would normally enter for the night. This ensured minimal movement by the animal over the ensuing few hours as a precaution against regurgitation. Release simply involved laying the opened bag on the ground and allowing the animal to leave at will.

5.3.2 Implanting procedure and precautions

After approximately thirty minutes in the capture bag following capture, in a cool place to calm the animal, the snake was grasped firmly, through the thin material of the bag, directly behind the head, and the head gently extracted. The emphasis during handling was to minimise any undue stress and possible injury to the animal in order to ensure, as far as possible, acceptance of the telemetry package and normal behaviour following release. For these reasons pinning the neck (e.g. with a 'jig' to a foam mat) was considered too stressful and not used. No restraining methods other then those using the hands and bag were found to be necessary during implantation. Only the head and neck of the animal were extracted from the bag, which served the dual purpose of preventing undue movement and, upon release of the head, meant that the

animal would naturally pull back into the bag, thus avoiding the need for further handling following the procedure. The prevention of undue movement was also an important safety precaution on occasions when telemeters had to be implanted in the absence of field assistants.

Positioning the telemetry package required first coating the forepart with a small amount of liquid paraffin. The use of a low irritant lubricant ensured that the package slipped between the jaws and into the oesophagus with ease. Holding the snake in the left hand, with the gular area between middle finger and thumb, the wax coated package was introduced to the animal and it was allowed to bite and hold it (Fig.5.3).

Fig.5.3 Introducing the telemetry package into the tiger snake (A2).(photo, S. Vanhoff)

The relatively thick wax coat on the package prevented damage to the short fangs and fragile mouth parts, and to the instrument. The recurved teeth usually held the package in place while allowing it to be easily worked to the back of the mouth; this part of the procedure was accomplished in only a few seconds with the fingers of the right hand. The package was then gently pushed into the throat with a pair of large blunt forceps (Fig.5.4). The lack of a sternum in snakes allows for the easy palpation of solid objects within the digestive tract and positioning the package into the rear of the stomach was a simple matter of gentle massage (Fig. 5.5). The whole procedure was usually completed in less than five minutes. Upon completion the bag was tied and left undisturbed for an hour.

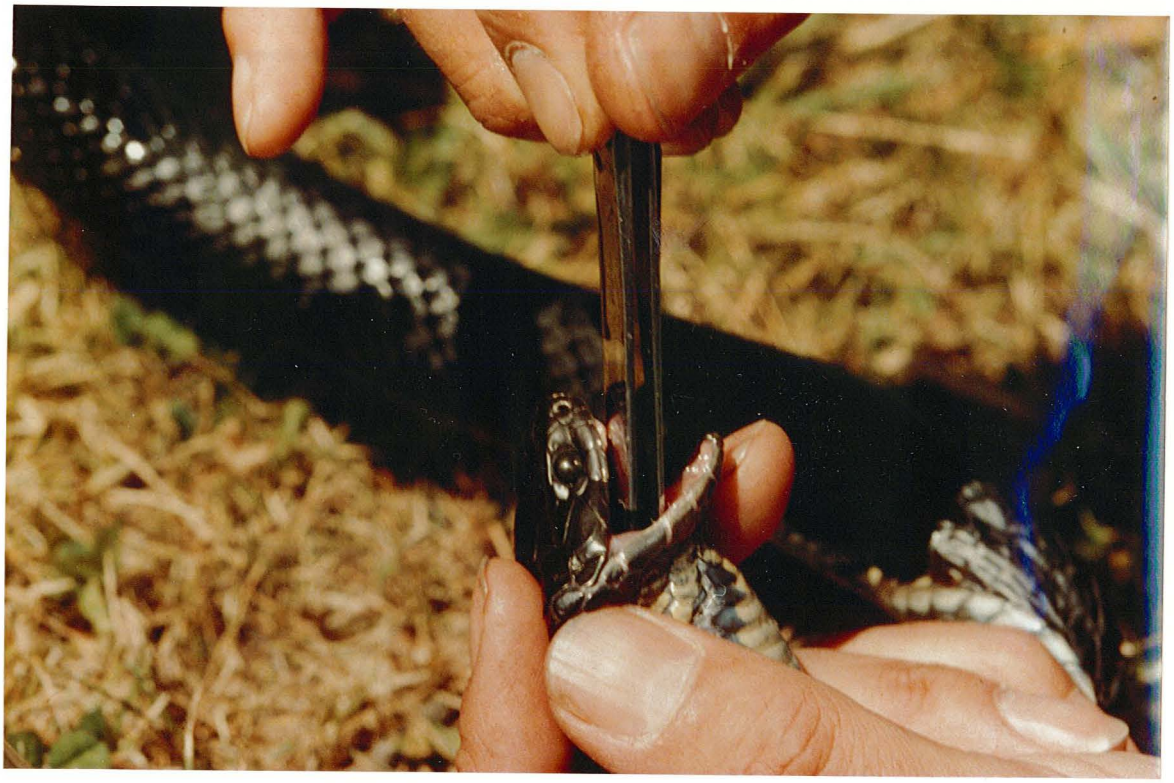


Fig.5.4 The package is gently pushed into the throat with a pair of large blunt forceps. (photo,S.Vanthoff)

During telemeter implantation and removal care was taken not to introduce lubricant to the hand holding the snake, or to the head, in order to maintain a firm grip. While holding the head venom tended to stream from the fangs, especially if pressure were inadvertently applied to the epithelium immediately behind the fangs or to the venom glands, and care was taken to ensure no broken skin was present on the hand holding the snake. Hands were washed thoroughly following each handling procedure. The option of using gloves was discounted as their use limits dexterity and makes it impossible to know exactly the minimum pressure required to restrain snake heads.

Fig.5.5 The lack of a sternum in snakes allows easy palpation of the package when in the snake. (photo,S.Vanthoff)

5.3.3 Duration and telemeter removal

Telemetry packages usually remained inside the Egg Island animals for eight days, and a package was carried by the first Lake Crescent animal for six days. At Egg Island this time included five field days followed by the three days required to transport animals to the University and determine eccritic body temperatures. Two Lake Crescent animals carried telemeters for three days only while in captivity.

In order to remove a telemeter the snake was grasped in exactly the same manner used for implanting. After securing the animal's head, a small dose of liquid paraffin (≈2ml) was introduced into the oesophagus via a small syringe and short (8cm) smooth plastic tube (size 14 intravenous catheter) with blunted tip. The tube was slowly inserted to its full length and the dose slowly given (Fig.5.6). The only danger to the animal from the relatively short tube lies in the possibility of it scratching the lining of the oesophagus; hence the reason for the blunted tip. The tube was kept short because of the possibility that a longer tube might penetrate the thin-walled oesophagus and lung if the snake should manage to struggle. There is little danger of accidentally administering into the trachea as the glottis of the snake is very obvious, positioned on the floor towards the front of the mouth, and therefore easily avoided.

Fig.5.6 Administering small dose of liquid parrafin prior to the removal of the package. (photo,S.Vanthoff)

Following administration of the liquid paraffin the neck of the snake was held in an upright position and the oesophagus gently massaged for several minutes. The telemeter was then located, through palpation, and by applying gentle pressure to the posterior end moved to the cardiac sphincter. In relatively small animals (Egg Island females), the sphincter represented the major obstacle to be overcome during the removal operation. It required some several minutes of gentle pressure with the back (blunt end) of the telemetry package before it would open sufficiently wide to allow the package through. This problem did not eventuate with females larger than 400 grams (Lake Crescent animals). It was then a simple matter of massaging it back along the oesophagus to a position immediately behind the jaws. In order to eject the package from the mouth it was necessary to release the head. However, this was not

as dangerous as it might appear because the bulge formed by the package in the neck of the animal prevented the snake from turning it's head. In order to keep the head under control the snake was laid on it's back, and held securely with the index fingers pressed up against the point of the jaw. From this position the package could then be eased out of the mouth with the thumbs (Fig. 5.7). At this point the snake could be released and allowed to eject the package itself, or alternatively, when it was desirable to keep control of the animal, the head was given a gentle shake to dislodge the package from the teeth. Releasing the snake while the package was in the throat did not result in expulsion, the package was simply reswallowed.

Fig.5.7 The package is removed. (photo,S.Vanthoff)

The telemetry method used in this study appears to have caused the snakes little or no harm as at least one animal fed with a telemetry package present in the stomach (A1) and two animals were observed to have fed within three weeks following removal (A2 and B2). Eight days were selected as the length of time telemeters would remain in the animals based on the likelihood of regurgitation increasing over time; and on the minimal time required to complete the field studies and determine eccritic body temperatures. If any animal had have avoided recapture, which none did, regurgitation should have occurred within a few weeks (Shine,1987b) and posed no long term ingestive/digestive problems.

5.3.4 Telemetry equipment and calibrations

During telemetry, the body temperature of the animal was continuously sampled every fifteen seconds and the data stored on computer. The field telemetry equipment included a telemetry package, directional antenna, receiver, custom-built digital data processor (digital pulse counter) and PC computer. Power was supplied by one of three heavy-duty sealed 12 volt batteries.

Fig.5.8 Telemetry package and magnet. (photo,S.Vanthoff)

Two telemetry packages were used in the study. Each included a low-powered, hermetically coated, TELONICS Inc.® CHP-IMP transmitter with magnetic switch, S2 temperature sensor, internal whip antenna and battery. Each package had approximate dimensions of 3 x 1.5 x 1cm (Fig.5.8), a total weight of nine grams and an estimated operational life of three and a half to four months at 37°C. Both telemetry temperature sensors were found to have a maximum temperature lag period of approximately one and a half minutes. The transmission frequencies were factory set at 151.210 (receiver channel 8) and 151.190 MHz (receiver channel 9). In order to minimise the risk of introducing disease or parasites from one site to another, the latter frequency was the only one used at Egg Island and the former frequency the only one used in Lake Crescent animals. The telemetry packages used weigh approximately the same as an

average three week-old laboratory mouse, a small to medium size food animal, and were thus easily accommodated by the snakes. The pyloric sphincter marked the maximum caudal position of the package in the unfed snake and was determined by dissection of road-killed animals to have a mean distance from the snout of 60.6% (sd=3.329, n=6) the SVL of the animal. Both telemeters functioned perfectly over the study period.

Both telemeters were calibrated during the week before commencement and the week following completion of the field study period. Calibrations were conducted in a thermostatically controlled waterbath using a Dobros® mercury reference thermometer with a maximum inaccuracy of ±0.03°C at 0°C. Upon recalibration, the channel 9 telemeter (Snake Island) was found to have suffered a maximum drift of 0.027°C at between 20-22°C, and the channel 8 telemeter (Lake Crescent) a maximum drift of 0.019°C at between 16-18°C. As both these differences lay within the accuracy range of the reference thermometer, and within the telemetry temperature sensor's manufacturer specified 0.1°C resolution, no post measurement corrections were required.

The directional antenna used in the study was simply formed from a normal yagi TV antenna cut in half. This resulted in a six element, 77.5 x 163cm antenna, which in the field was mounted on top of a 1.5 x 0.03m steel tube driven approximately thirty centimetres into the ground. While snakes were active above ground this resulted in a maximum receiving range of approximately fifty metres (±10m) depending on background interference, rainfall and density of cover. This range was considered adequate in the circumstances as the vegetation was often very thick at the Egg Island site. The maximum distance travelled away from the night-time retreat, by any of the telemetered females on any one day, was forty-five metres. Most days the animals remained within thirty metres of the antenna; although reception was often lost due to moisture when snakes were in the marsh area or under wet vegetation. The antenna was placed at one of three locations around the edge of the home-range; the actual position depending on the time of day and on the position of the animal. Care was taken to hide the antenna from the animal either through positioning it behind available vegetation or by simply laying it on the ground pointed at the animal.

A tent was used to house the receiver, digital data processor, computer and batteries. This was positioned approximately twenty-five to thirty metres away from each burrow entrance and where it would not be obvious to the snakes. The coaxial cable attaching the antenna and receiver was twenty five metres long, longer than needed for fixed-site reception, as additional length was necessary for determining the position of hidden animals through triangulation.

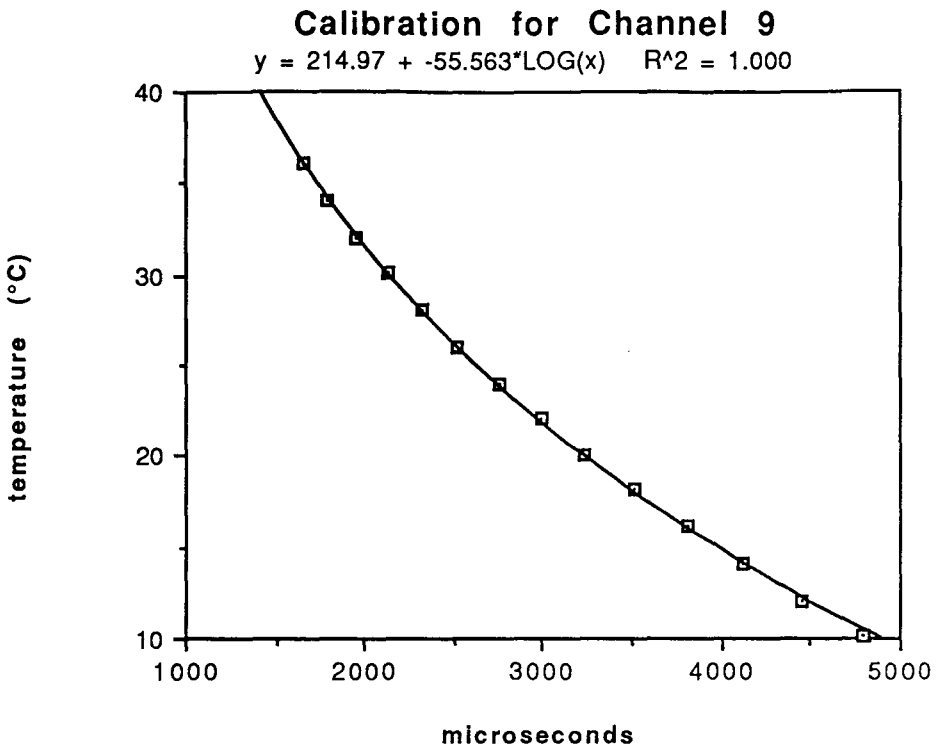
Two receivers were used during the study. The first was a nine-channel Austec® Model 31 Tracking Receiver used for all but the last field trip where it was damaged. The replacement receiver was a Yaesu® VHF/UHF, FRG-9600 Communications Receiver with a frequency range of 60-905 MHz. The former required constant adjustment in the field and was subject to a good deal of background noise (especially during wet weather). Hence, for most of the field study period it was necessary to adjust reception through the night in order to secure night-time values. The latter receiver required very little adjustment.

The receiver output was in the form of an audible beep and a signal which was recovered and converted into machine readable form for data conversion and storage by computer. This was achieved through the development of a digital data processor capable of squaring and counting the pulse intervals (for details of the circuit refer to Appendix 2). The length of the interval between pulses was used to generate a number which was inversely proportional to temperature; i.e. the pulse repetition rate increased with increased body-temperature. The pulse interval was sampled every fifteen seconds and storage of the large amounts of data thus generated required a PC computer with a relatively large data storage facility; a Tandy® 1400HD PC was used for this purpose. A simple programme was written by Mr. Paul Waller (Central Science Laboratory, University of Tasmania) in BASIC to perform the data sampling which is listed in Appendix 3.

The raw telemetry data was converted to body-temperature values using sensor specific polynomial calibration factors (Fig.5.9).

5.4 MICROCLIMATE MEASURING AND MONITORING PROGRAMMES

Microclimatic variables pertinent to calculating snake surface and body temperatures (T_s and Tb) were monitored concurrently with the telemetered animal's body temperature for periods of five days. These were monitored immediately adjacent to, and within, each animal's home-range. The microclimatic variables monitored included: inground temperature (T_g), ground heat flux (Q_G), ground surface temperature (T_r), mean wind speed at a height of 1.6m ($\overline{U}$) and at a snake height of 2cm ($\overline{u}$), wind direction (V), relative humidity (RH), air temperature (T_a), down-welling global radiation (K↓),



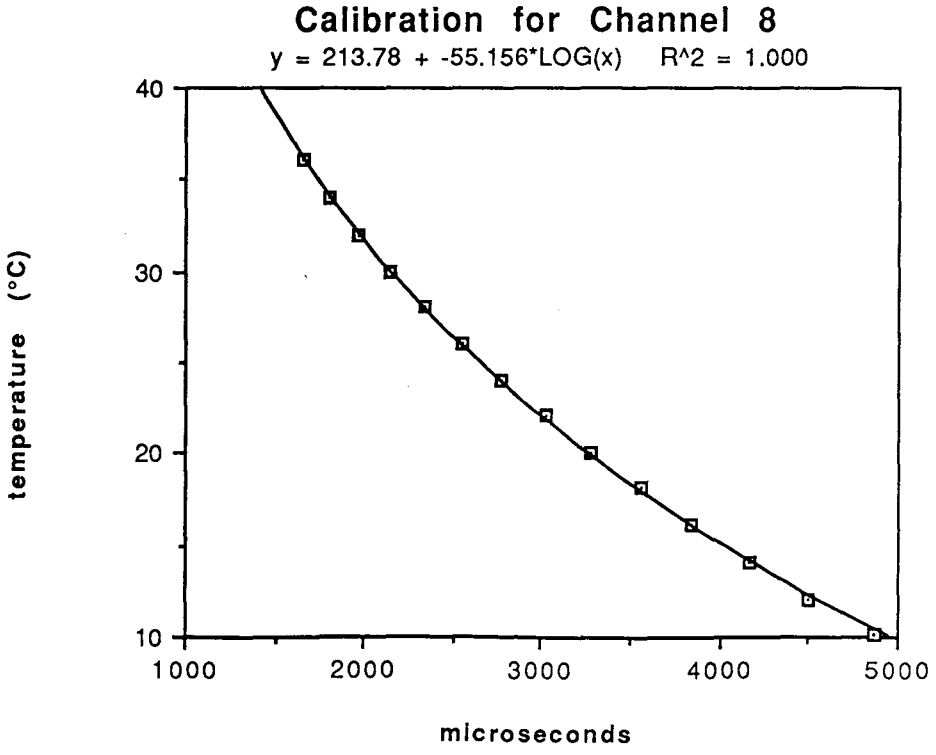


Fig.5.9 Calibration curves for temprature sensitive radio telemeters.

down-welling longwave radiation (L↓) down-welling diffuse radiation (D), percent cloud cover (c) and rainfall. In addition, ground-surface albedo (αr), slope, aspect and sky-view factor at basking sites and day-time retreats were recorded in order to determine the amount of solar energy available to the animal.

5.4.1 Soil instruments, methods and assumptions

T_g's were measured using Campbell Scientific Instruments® (C.S.I.) Model 101 thermister probes (with a maximum digitizing and probe component error ±0.5°C). Although the probes are supplied as water-proof units, seams were further water-proofed with a silicon sealant. The thermisters were water-bath calibrated using a Dobros® mercury reference thermometer: before and after the field study period. During the latter period the probes were thrice calibrated in sealed-room air against a Cassella® Assman-type reference thermometer. Maximum drift was determined to be 0.35°C in only one probe at the cessation of field-work. The T_g data were corrected automatically for error on sampling using the C.S.I. CR21 data-logger offset facility.

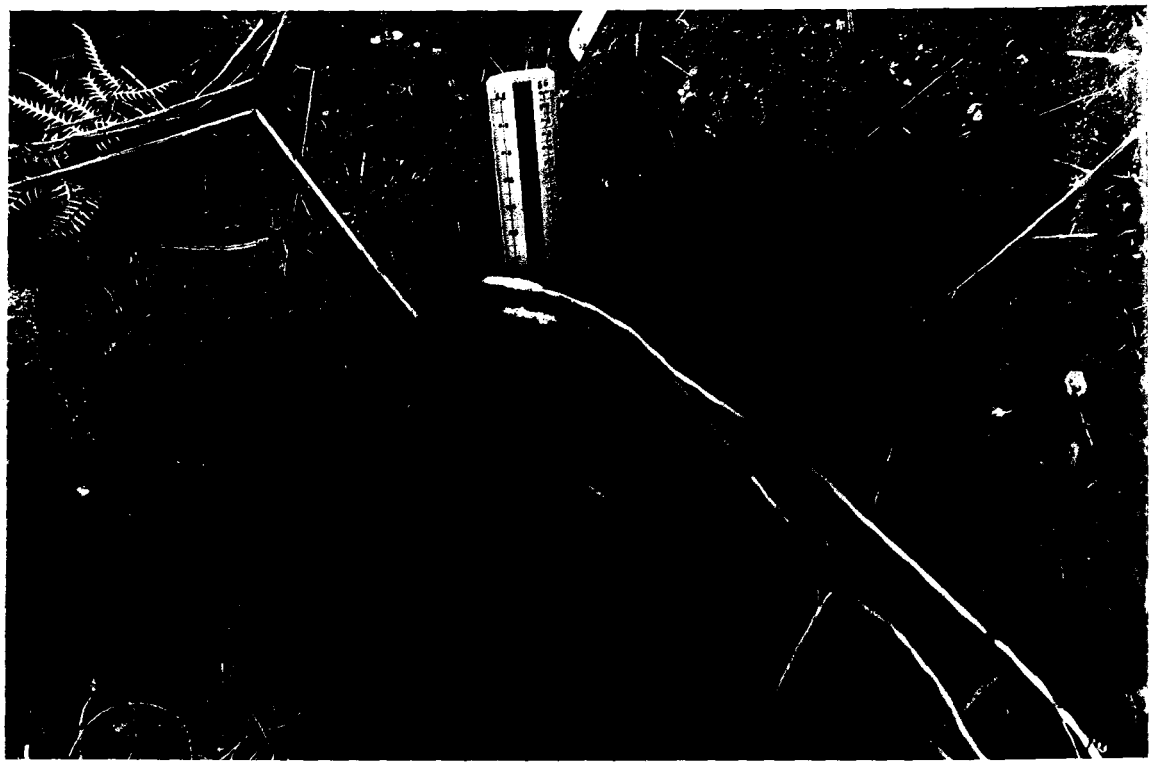


Fig.5.10 Installation of ground temperature thermisters (T_g).

T_g thermister probes were placed as close as possible to night-time retreats. In order to avoid disturbing sequestering snakes; this usually meant that placement was no closer than three metres. Only sites subject to similar solar exposure and in similar situations as retreat-sites were selected for this purpose. The thermisters were installed at depths of 2, 5 and 20cm (Fig.5.10) and were attached to a C.S.I. CR21 data-logger

down-welling longwave radiation (L↓) down-welling diffuse radiation (D), percent cloud cover (c) and rainfall. In addition, ground-surface albedo (αr), slope, aspect and sky-view factor at basking sites and day-time retreats were recorded in order to determine the amount of solar energy available to the animal.

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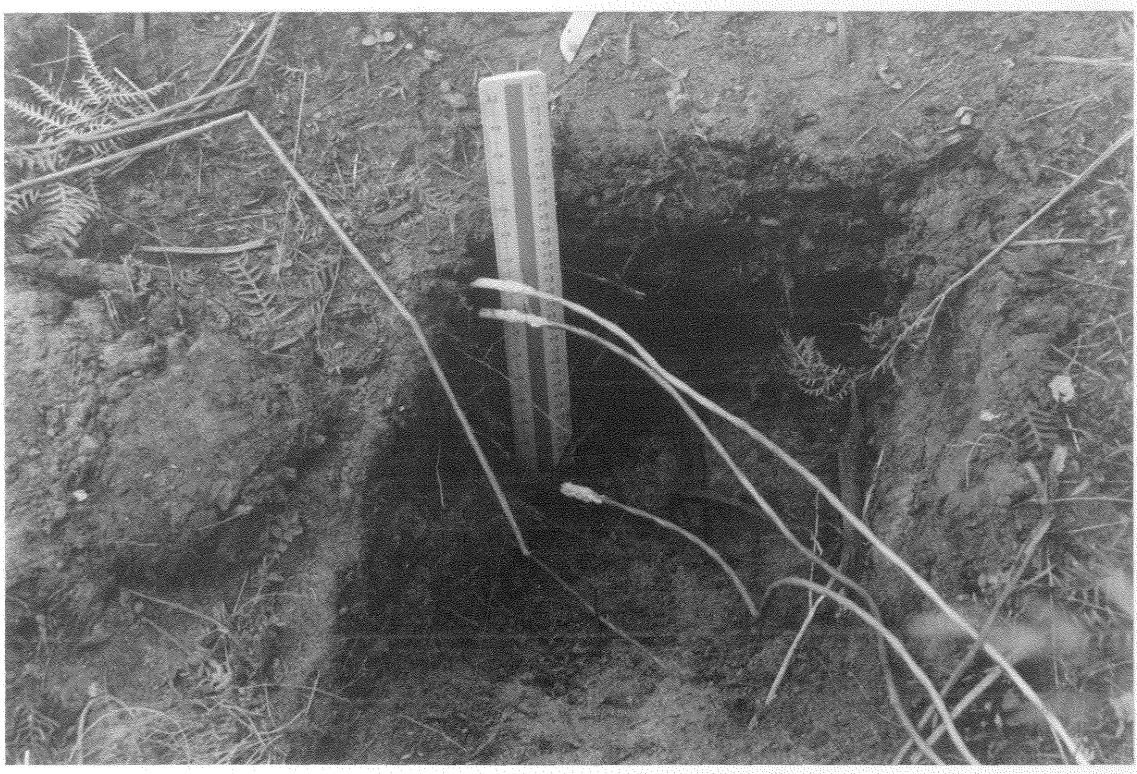

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programmed to sample the soil temperature every ten seconds and to calculate mean T_g's every fifteen minutes. The data were stored on a portable tape-recorder. Both the data-logger and tape-recorder were housed inside a C.S.I. weather-proof case. Both were checked for function every two hours between 0700 and 1900 hours EST.

Q_G's were measured using three new Middleton® Model CN3 soil heat-flux plates supplied with factory determined calibrations. These were carefully placed five millimetres under the soil surface in three different situations within the telemetered animal's home-range. Sites chosen for this purpose were either those used by the animal for basking and day-time retreat or, if animals moved about extensively, those assumed to be representative of the night-time retreat-site and basking-sites. Whenever possible two of the plates were positioned at the side of, or under, basking-pads and the leads carefully hidden. The heat-flux plates were attached to the C.S.I. CR21 data-logger and the data sampled and stored in the same way as the T_g data.

For modelling purposes, inground T_g values were assumed to represent the entire study area. This assumption was based on the homogenous levee soils and similar northerly aspect along the entire south shore of the Egg Island canal site. Thus, T_g values measured at a telemetry site were assumed to be representative of inground values available to all sequestering animals where retreat-sites were in similar situations. Q_G's were not assumed to be similar to each other, even when in close proximity, due to the highly variable sky-view factors.

5.4.2 Screen instruments, methods and assumptions

The term screen refers here to the frame upon which a Stevenson's screen, with T_a and RH sensor, is mounted. Screen height refers to the standard height (1.6m) used by the Bureau of Meteorology.

The screen variables monitored in this study included T_a, RH, K↓, V and $\bar{U}$. The screen height used was the Bureau standard and the frame was a T-shaped steel frame on which to mount the instruments (Fig.5.11). The screen carried the following: a C.S.I. Model 201 T_a thermister probe and RH (±2%) sensor; a Kipp and Zonen® CM11 pyranometer used to determine K↓; a Met One® Model 024 wind direction sensor and Model 010 cup anemometer with an inertial start-up speed of $0.44ms^{-1}$. The screen also carried a C.S.I. CR21 data-logger and all data was sampled, processed and stored using the same method as the soil data. The screen was placed approximately thirty metres away from retreat-sites, outside of home-ranges, in an open position not visible to the animals. It was carefully levelled and pegged securely. Data-logger

Fig.5.11 Screen instruments, pyrgeometer and diffusograph in use at Egg Island sub-site 2. The township of Franklin can be seen in the background.

function was checked two-hourly and the levelling of instruments checked daily or after high wind.

The T_a thermister - RH C.S.I. 201 sensor was calibrated in sealed room air and found to exactly correlate with a Cassella® Assman-type reference psychrometer, before, once during and following the field study period. Additional T_a and RH readings were taken when animals were discovered further than 300m away from the screen using a Brannan® Model BS 2842 psychrometer. This latter instrument was also calibrated as for the C.S.I. 201 sensor.

Also attached to the screen data-logger, and recorded and checked in the same way, were instruments for measuring L↓ and D. These were: an Eppley® Model SF3 pyrgeometer (L↓) which was mounted on top of a 1.4m galvanised iron post (Fig.5.12); and a second Kipp and Zonen® CM11 pyranometer mounted onto a diffusograph frame to measure D (Fig.5.13). This was placed on a 1.1m high wooden table at the study site with the long-axis aligned to point true north. The diffusograph frame used is similar in design to an Eppley frame, but differs in that the mat-black painted occluding ring forms a complete circle around the pyranometer. The frame was constructed following a design by Dr. M. Nunez.

Fig.5.12 The pygeometer to measure longwave radiation (L↓)

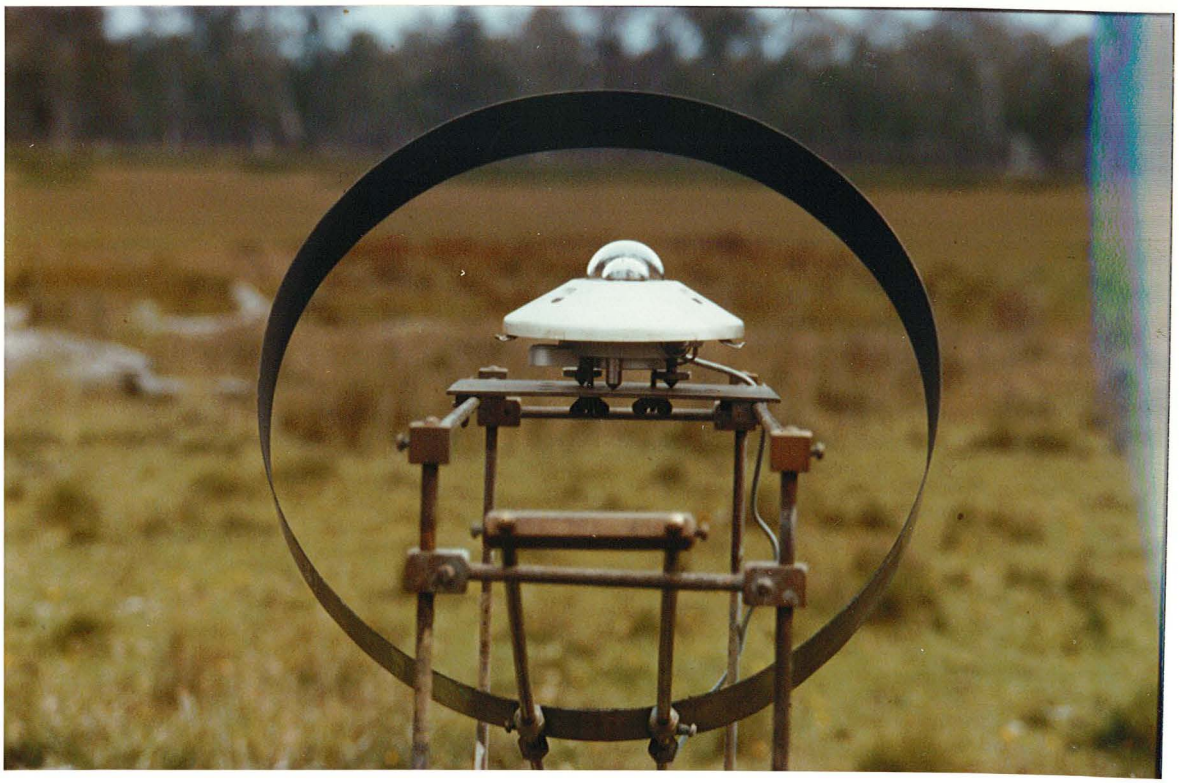


Fig.5.13 The pyronometer mounted into a difusograph to measure difuse sky radiation (D) (design Dr.M.Nunez).

As the diffusograph shading ring obscures an area of sky larger than the solar disc, the raw D data required adjustment by a geometric correction factor to determine true D values. The method used for this purpose was that of Iqbal (1983), which provides both a geometric correction and an additional factor to account for cloud cover (c). The geometric correction was adjusted by: +0.07 for cloudless skies where $c \leq 10\%$, +0.04 for partly cloudy skies where $10 < c < 90\%$, and +0.03 for overcast skies where $c \geq 90\%$. For details of the computer programme used to determine D correction factors refer to Appendix 4.

As it was not possible to monitor the microclimatic variables as experienced by a snake from screen height at distance from the animal's position, it was assumed that T_a, RH and V as monitored by the screen were pertinent to observed thermoregulatory response. It must also be assumed that methods used to monitor radiation variables at screen height are valid when applied to ground-level and calculated for sky-view factor and albedo.

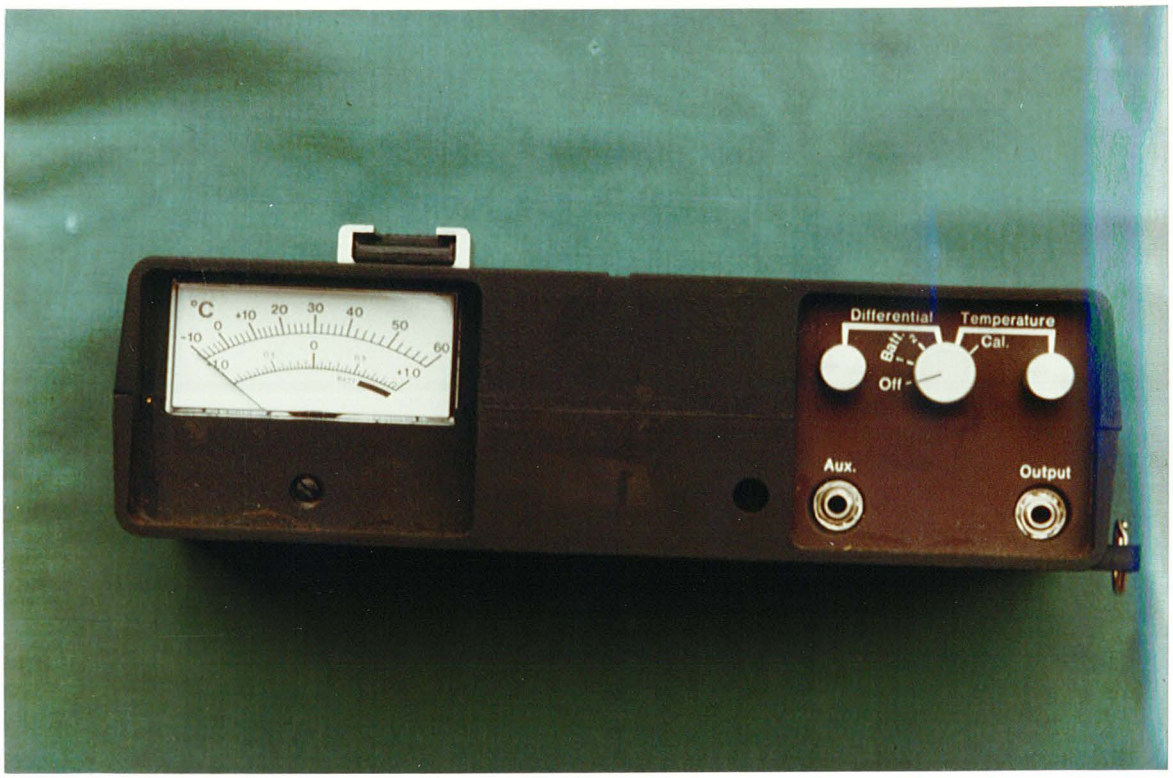


Fig.5.14 Hand held narrow field (2.5°) infrared thermometer for ground surface temperature readings (T_r).(photo,S.Vanthoff)

5.4.3 Surface instruments, methods and assumptions

Only the T_r and $\bar{u}$ of basking-pads and day-time retreats of non-telemetered adults were measured and recorded. Telemetered females were not used for this purpose as it was found to be virtually impossible, using the available instruments, to achieve T_r

and $\bar{u}$ measurements without disturbing the animals. The instruments used for the surface measurements were a Barnes® Model 14-220-1 hand-held narrow-field (2.5°) infrared thermometer (Fig.5.14) and a Selbys Scientific® Model TA 3000 hot-wire anemometer (Fig.5.15).

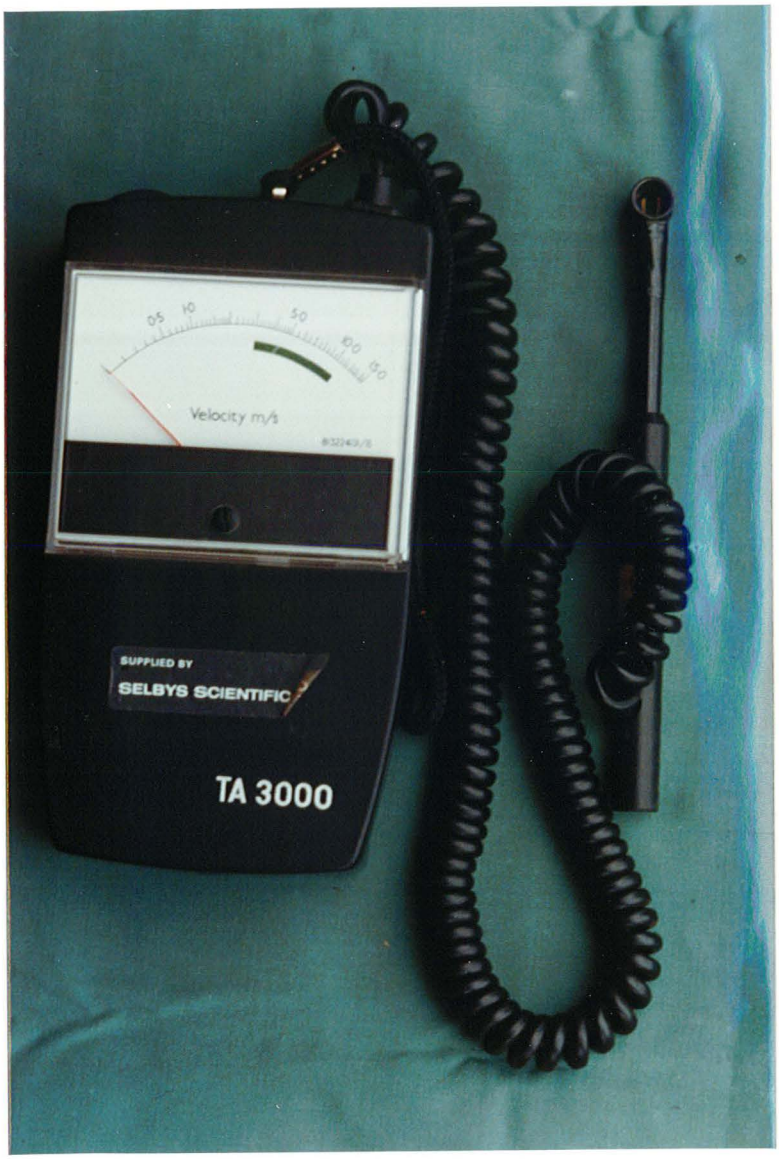


Fig.5.15 Hot-wire anemometer used for 2c.m.high surface wind readings ($\bar{u}$).

The method was to undertake a two-hourly search for all females on basking pads in the area and, when found, to measure T_r (from a height of 0.5m) and $\bar{u}$ on and over the pads. Each of these variables were recorded as a mean of three readings; this was found to be necessary due to microtopographic heterogeneity at many of the pads used. Pads also often displayed several very different T_r's due to the extended

basking postures of animals in early and late warm-up phases. The hot-wire anemometer proved to be very sensitive to wind direction and required rotation until a maximum value was found. The $\bar{u}$ value was measured over a position on the pad which corresponded to the middle of the animal's body.

For the purpose of the study, the importance of surface emissivity in characterising exact surface temperature using an infrared thermometer was ignored and surface emissivities were assumed to equal one. The relatively small diameter of a hot-wire anemometer would not be representative of the exact convective conditions as experienced by the snake; due to the larger diameter and therefore boundary layer of the latter. However, the purpose of the wind readings at two centimetres was to determine if snakes were minimising wind exposure at snake-height (i.e. $\bar{u} \leq 0.5 ms^{-1}$), and thus experiencing free convective heat exchange. The instrument proved adequate for the purpose.

5.4.4 Cloud-cover and precipitation

Cloud amount and type were estimated as tenths of visible sky cover at three levels: low, middle and high, every two hours between 0700 and 1900 hours EST. Rainfall was measured using a 203mm rain-gauge which was placed in an area open to the sky. The gauge was checked and emptied each twelve hours: at 0700 and 1900 hours EST.

5.4.5 Mapping

Mapping was only undertaken at the Egg Island site and was in two forms: the first, in estimated form prior to commencing each telemetry study; the second, in detailed form only after each study was completed. Detailed mapping could not be achieved prior to telemetry studies as it would firstly, have resulted in disturbing animals, and secondly, the extent of the area required for mapping could not be known until the habitual movements of animals had been determined. A further limiting factor on when to map was the common habit of two adult females occupying overlapping home-ranges; possibly due to limited availability of suitable sites. Thus, detailed mapping would have resulted in disturbing at least one adult female had it been undertaken prior to the telemetry.

Each animal selected for telemetry was observed for a minimum of forty-eight hours, prior to capture, in order to determine normal activity patterns. On capture of each animal for implantation, the home-site was measured for distances between the sites

most frequently used by the animal for basking or retreat. More detailed mapping was not possible at this stage as it was necessary to implant and release the animal within two hours of capture.

Following the completion of the telemetry studies at each sub-site, each home-range was marked-off by string and divided into one metre quadrats. The quadrats were then mapped for microtopographic features, including: mean slope, mean aspect, ground cover and height (Fig. 4.4a, b, Fig. 4.5a, b). Each home-site was also mapped for mean T_r (Fig.6. 17a, b), at solar zenith angles of between thirty and forty degrees, during the morning and again in the afternoon. However, due to the experimental design requiring the placement of each telemetered animal into a temperature gradient within twelve hours of capture, it was not possible to map the mean surface temperature differences in detail until after completion of the telemetry studies. The latter was accomplished during the first week of March, within four days following the capture of the last telemetered animal.

Microtopographic maps were needed to evaluate the affect of potential convective shields on animal energy budgets. Knowing the mean temperature differences within each home-range was considered important for two reasons: the first being that it could not be possible to know if animals were optimising thermal environments without these values, and secondly, the maps allowed for calculation of pad T_r's post-study from field notes. The latter, by relating the T_r values of a fixed point, unoccupied by the snake, to that of the mean difference between the two surfaces. In this way it was possible to estimate T_r of basking pads without disturbing the telemetered animals.

Each mapped area included the combined home-ranges of two snakes. The combined mapped surface area of the S1 pair (A1 and C1) encompassed a surface area of $88m^2$, and that of the S2 pair (A2 and B2) a surface area of $100m^2$ (Fig.4.4a, b respectively).

5.4.6 Surface albedo

Surface albedo (αr) was determined for all basking pads used by the animals during the study. The method involved inverting a pyranometer over the pad at a height of thirty centimetres and dividing the mean reflected value by the mean value of K↓ (Wm^{-2}). The αr was calculated in this way for when the sun was low ($\approx 30°$) and when overhead, and only on clear days with <10% cloud-cover. The latter consideration meant that αr could only be calculated for both solar positions on four of the field study days at the Egg Island site; as most field-study days experienced >10% cloud cover.

Due to the lack of a spectro-reflectometer, it was also attempted to determine snake surface albedo (αs) by the latter method; in which only dead (road-killed) snakes were used. The snakes were coiled to form a disc of a known radius on a uniform background and a pyranometer was suspended twenty centimetres above the snakes and the value recorded. However, no geometric correction factor could be found which would satisfactorily correct for αr. Hence, only estimated values of αs where determined; the mean values for road-killed animals with different skin colours were ≤ 0.182 (sd = 0.0146, n = 6) reflectance (solar angle 30-40°) and ≤ 0.18 reflectance (solar angle >60°). As these values were the highest mean combined values of both αs and αr, and as αr was greater, they represent extreme and overestimated values for αs.

6 DATA ANALYSIS

6.1 INTRODUCTION

The results presented in the following were selected on the basis of their relevance to subject discussion and are mainly taken from the four Egg Island telemetry study periods where environmental effects can be related to snake body temperature (Tb). The results used are confined where possible to three consecutive days, from each study, where both Tb and the microclimate records are both virtually uninterrupted. Confining the results used to three days for each study was found to be necessary due to the volume of data and because of the need to examine all climatic variables collectively as they all influence Tiger Snake thermoregulatory behaviour.

All climatic variables that were determined to show strong positive correlations with Tb have been dealt with individually and in some detail. However, wind direction is not discussed separately, as it was determined to have no correlation with Tb at screen height, and is discussed in relation to the other variables where applicable. Relative humidity is not discussed as it showed only negative correlation with Tb, as measured at screen height, and this can be explained by evaporation of early morning dew, as animals emerged from night-time retreats, and rainfall. As the available data for this variable could not be otherwise associated with Tb it is not dealt with further.

The results of each measured variable are discussed separately in order to facilitate an understanding of their relationship with the snake and of their effect on the energy budget of the animal.

The derivation of empirical and biophysical relationships is discussed in the final Chapter.

6.2 DATA PROCESSING AND COMPILATION

The data-logger tapes were down-loaded using C.S.I.® PC 201 software and stored on disk. The computer stored Tb data were calculated for fifteen minute means and dumped to disk. The collective data was then concatenated on the SPARC Sunstation 'GEO' and files were generated using Microsoft EXCEL® (Version 3.0). Spread-sheet data were compiled from data-logger, PC computer and field notes for further processing.

6.3 BODY TEMPERATURE PROFILES

This section shows diel rhythmicity in Tb in free-living snakes on Egg Island over 72 hours for each animal. In order to interpret the results presented in this chapter, an appreciation of the thermal needs of the study animals is required, therefore, the mean eccritic Tb's and voluntary thermal limits (VT's) are dealt with first.

6.3.1 Eccritic means and voluntary thermal limits

The VT limits and mean eccritic Tb's for the four Egg Island and three Lake Crescent animals, together with the sampling dates, are presented in Table 6.1. These data clearly show non-gravid Lake Crescent females (Fig.6.1a, b) to have relatively low mean eccritic Tb's when compared to the non-gravid Egg Island animals (Fig.6.2a and b). They also show a higher mean eccritic Tb in the gravid Lake Crescent female (Fig.6.1c) than for non-gravid females from the same area. Both gravid females had similar mean eccritic Tb's (Figures 6.1c and 6.2c) and both showed slightly higher eccritics than any of the non-gravid animals. The Egg Island gravid female displayed the highest mean eccritic Tb recorded. Note the similarity between the plotted Tb's of both gravid animals which appears to belie their geographical isolation.

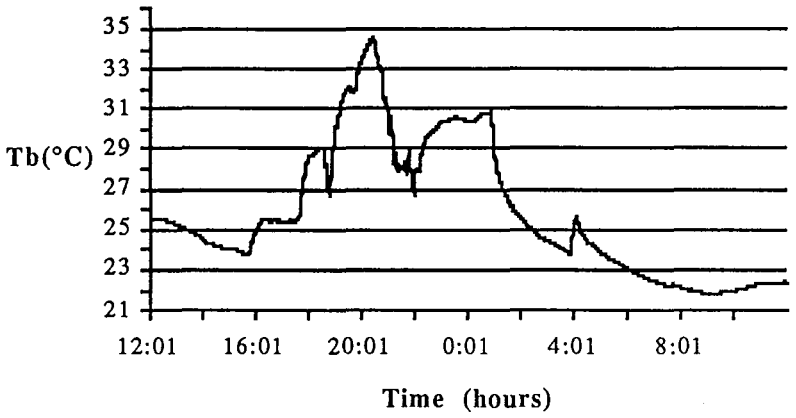
Table 6.1 Mean eccritic body temperatures and voluntary thermal limits of all telemetry study animals

DATE	ELEVATION	VT_{min}(°C)	VT_{max}(°C)	ECCRITIC MEAN (°C)
14.01.92	Sea-level	27.82	34.79	31.49
24.01.92	830m	21.82	34.54	25.82
02.02.92	Sea-level	26.17	34.88	30.57
07.02.92	830m	22.02	30.47	25.48
18.02.92	Sea-level	24.19	35.72	31.04
21.02.92	830m	24.36*	35.68*	31.68*
02.03.92	Sea-level	24.75*	34.34*	32.09*

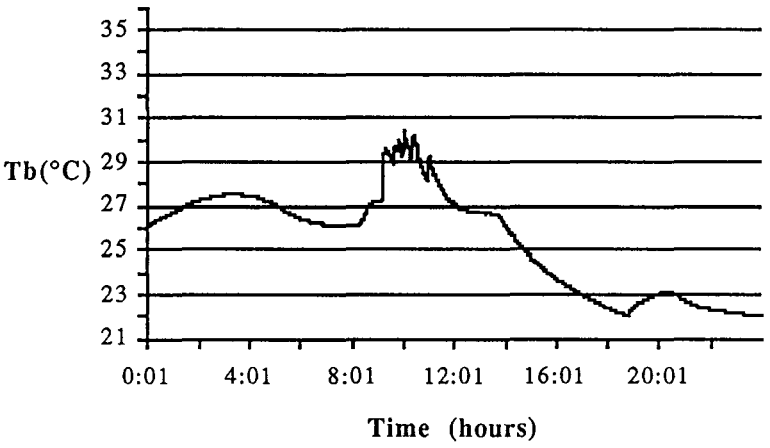
* Gravid female body temperatures

The VT_{max}'s shown in Table 6.1 are maximum point values only and, as these temperatures were not achieved by any animal measured in the field, they may only represent temperatures the animals are willing to tolerate while stressed by captivity; they may not be levels of Tb that would be tolerated by free-living animals. The data presented in Table 6.1 are isolated 24 hour samples and, due to the small number of animals measured, must be interpreted with caution. Nonetheless, the elevational

a) Crescent 1. Minute Tb's (24.01.92)



b) Crescent 2. Minute Tb's (07.02.92)



c) Crescent 2. Minute Tb's (21.02.92)

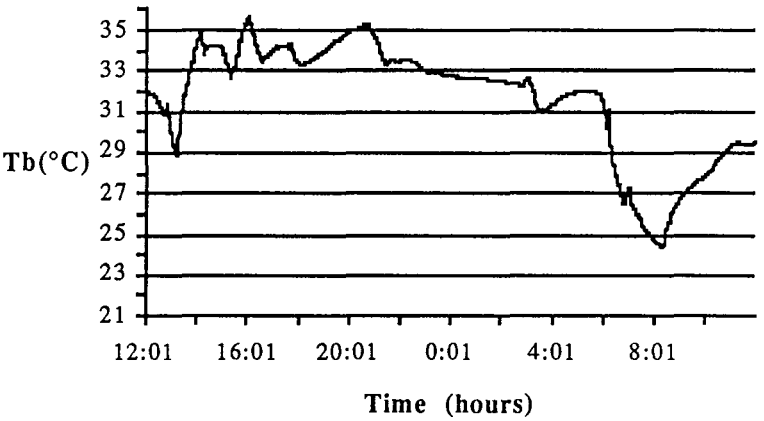
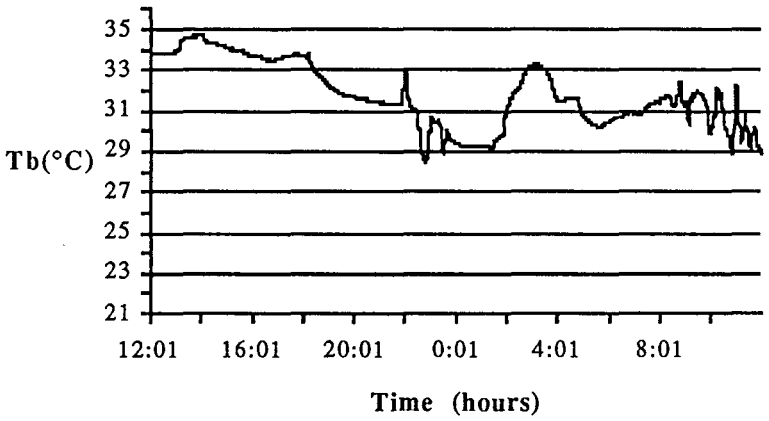
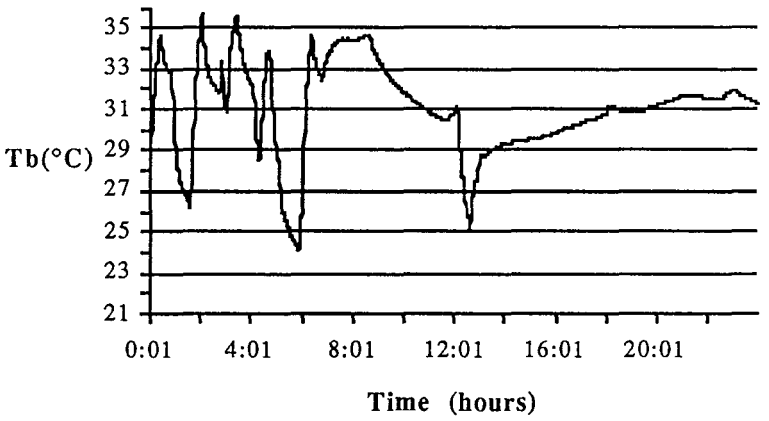


Fig. 6.1 Eccritic body temperature profiles of non-gravid Lake Crescent females (a.and b.) and a gravid female (c.) recorded over 24 hours in a temperature gradient chamber.

a) Huon 2. Minute Tb's (14.01.92)



b) Huon 4. Minute Tb's (18.02.92)



c) Huon 5. Minute Tb's (02.03.92)

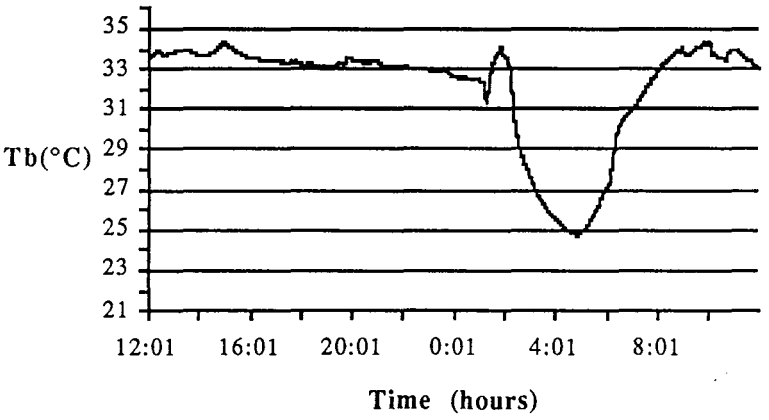


Fig. 6.2 Eccritic body temperature profiles of non-gravid Egg Island females (a.and b.) and a gravid female (c.) recorded over 24 hours in a temperature gradient chamber.

differences observed in the non-gravid animals may account for the low numbers found to be active during mid-summer at Lake Crescent. Lower eccritic Tb's in animals at higher elevation, should this be the case for all females in the population, can be seen to be of advantage in the relatively cool and seasonally extreme environment by permitting snake activity during the spring and autumn.

The differences in eccritic Tb's shown by the gravid and non-gravid Lake Crescent animals may be indicative of a seasonal shift in eccritic temperatures. Many more snakes were active on the date the gravid female was captured than on previous visits: an average of two snakes per hour were sighted during late February compared to one per 3.5 hours on the previous occasions. However, a change in physiologically optimal temperatures of this magnitude (approximately six degrees) for the whole population is unlikely over such a short period (14 days) and the data suggest the gravid animal had a higher mean temperature requirement than non-gravid females in the same locality.

6.3.2 Field telemetry data

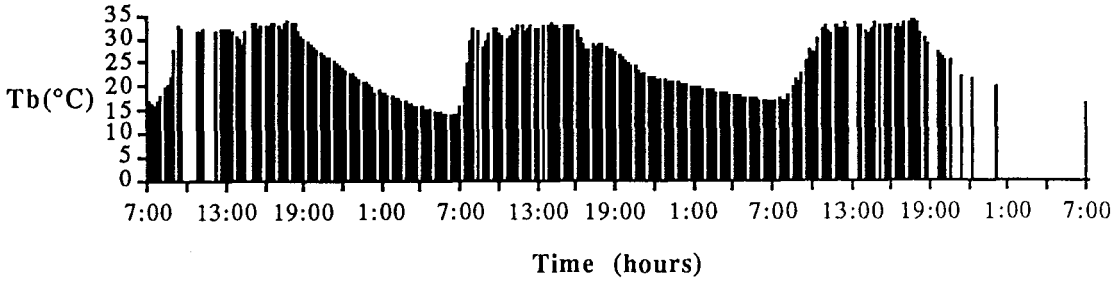
The Tb profiles of free-living Egg Island females are presented in Fig. 6.3. Gaps in the profiles correspond to occasions when reception was weak either due to rainfall or dew (especially at night) or to when animals were in dense vegetation during the day. The shape of the Tb profiles can be related to the weather conditions at the time and these relationships are discussed in detail in Section 7.3. The mean, maximum and minimum Tb's, together with the times these values were recorded, are listed in Table 6.2.

Table 6.2 Daily mean, maximum and minimum summer body temperatures (°C) of adult female Tiger Snakes during twelve days at Egg Island

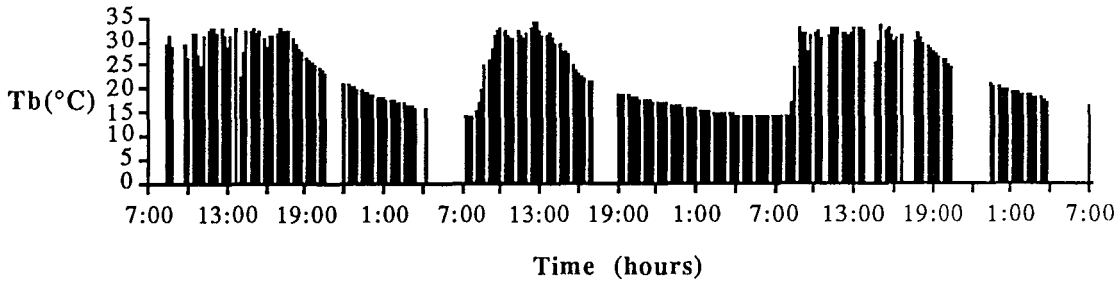
DATE	Tb Max.	TIME	Tb Min.	TIME	MEAN	SD
10.01.92	33.99	17:34	15.51	07:18	24.23	6.10
11.01.92	33.30	13:55	13.79	06:38	23.96	6.54
12.01.92	34.12	17:19	16.28	07:10	24.11	6.50
28.01.92	33.28	16:57				
29.01.92	33.93	12:24	13.94	07:33	22.49	6.53
30.02.92	33.51	11:08	13.76	07:18	22.34	7.97
13.02.92	33.49	14:36	16.31	11:12	20.98	4.69
14.02.92	33.88	13:05	13.82	09:30	22.72	6.20
15.02.92	34.19	11:09	12.49	08:13	25.77	6.1
27.02.92	33.28	15:34	13.44	07:29	25.28	7.21
28.02.92	33.1	10:04	13.87	08:04	23.08	7.39
29.02.92	32.74	17:26	13.97	08:17	23.75	6.84

Mean Tb maxima = 33.57 , Mean Tb minima = 14.29

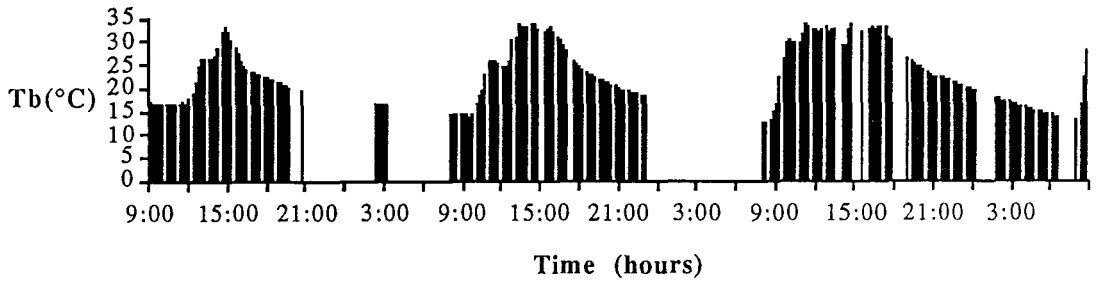
A1. 15 MINUTE MEAN BODY TEMPERATURE (10-12.01.92)



A2. 15 MINUTE MEAN BODY TEMPERATURE (28-30.01.92)



B2. 15 MINUTE MEAN BODY TEMPERATURE (13-15.02.92)



C1. 15 MINUTE MEAN BODY TEMPERATURE (27-29.02.92)

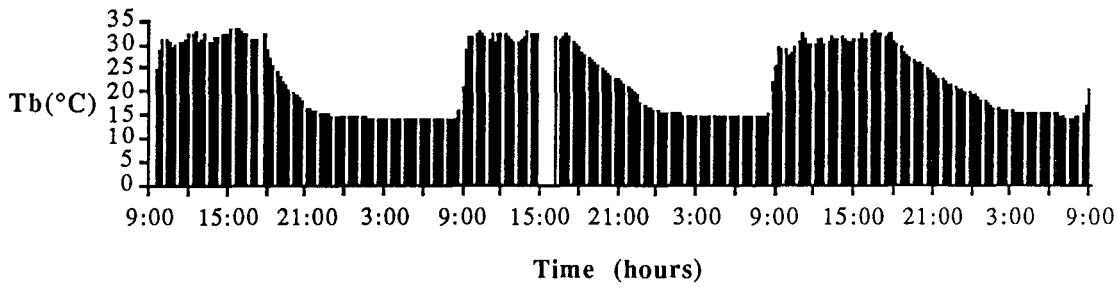


Fig.6.3 Body temperature profiles over 72 hours for free living Egg Island females A1, A2, B2, C1

These data show minimum Tb to usually occur in the early morning, except on days with little incoming radiation, and most often to occur on or just prior to the snakes emerging from night-time retreats. The relatively late minimum Tb's recorded on days 13-14.02.92 coincided with a late emergence by all animals in the area. This is thought to have been due to a moisture laden cool southerly air flow and overcast sky conditions which had persisted for several days. All maximum Tb's shown are surprisingly similar and demonstrate the ability of these animals to reach eccritic temperatures even in adverse weather conditions.

6.4. RADIATION

6.4.1 Relationships

Diffuse solar radiation (D) and solar zenith angle (z) (calculated using the Applied Environmetrics Tables of Beer, 1990), enabled calculation of the direct component (I) of global radiation (K↓) from:

$$K\downarrow = I \cos z + D$$

where:

$$I = K\downarrow - D / \cos z$$

34.

The grouped values for I , D, K↓ and L↓ were then plotted against Tb to determine the relationships with Tb (Figures 6.4a-11a). The strength of the relationships for all four forms of radiation, in both grouped and single data sets, were then tested using Pearsons correlation coefficient r (Figures 6.12-13a, b). From the grouped sets the coefficients of determination indicated K↓ (r^2=0.5) and K↓+L↓ (r^2=0.536) to be more closely related to Tb than either D (r^2=0.18) or L↓ (r^2=0.08) when evaluated separately; and similarly there was no difference between I and K↓.

The relationships thus derived, showed the grouped data sets for K↓ (Fig.6.12a) and for total incoming radiation (K↓+L↓, Fig.6.12b) both to have highly significant relationships with the rate of Tb increase. Further, K↓+L↓ for the overall data sets is more closely associated with Tb than is K↓ alone.

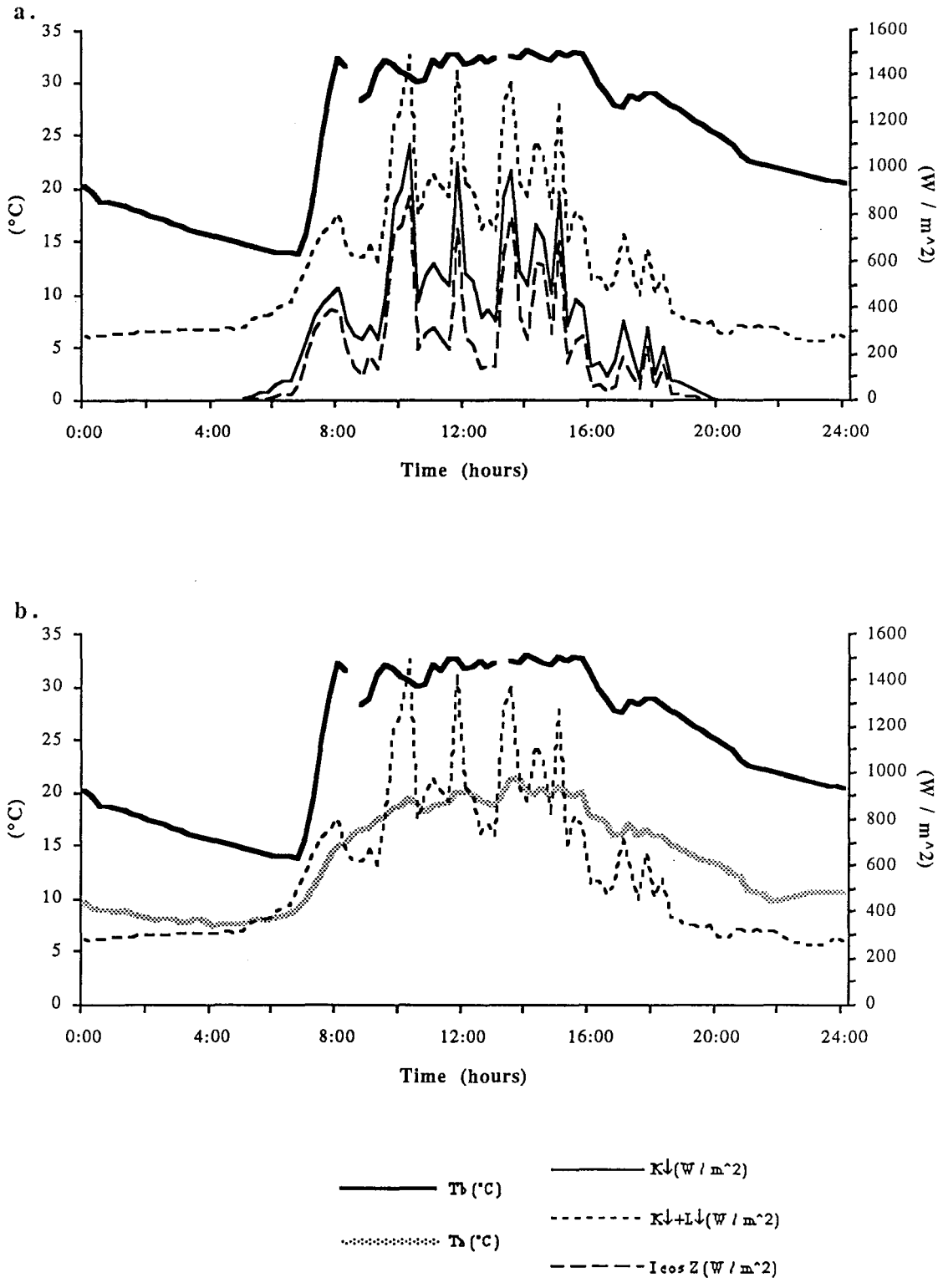


Fig.6.4 Tb profile over 24 hours, with different forms of incident radiation (a) and with air temperature (b) (11.01.92).

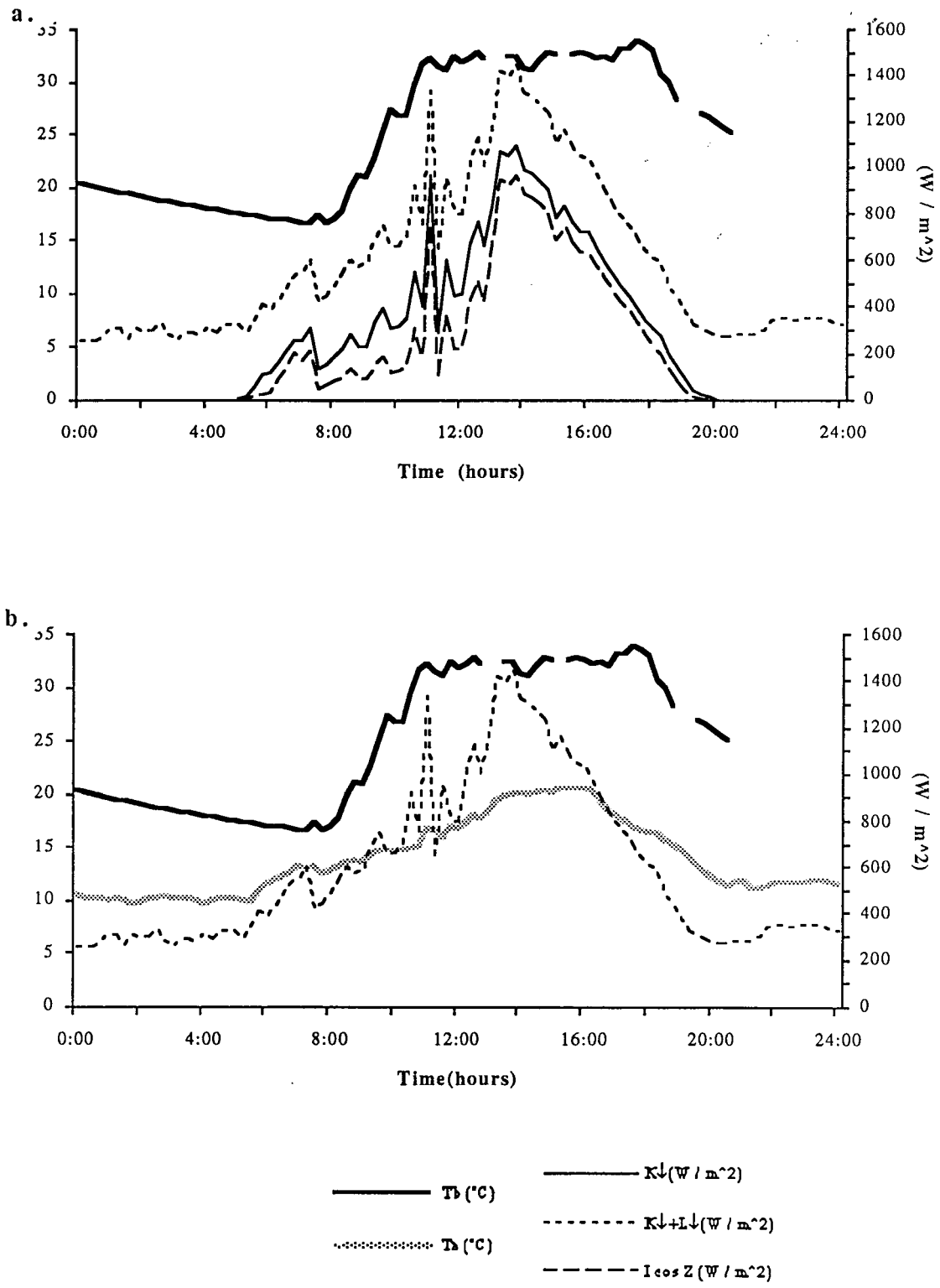


Fig.6.5 Tb profile over 24 hours, with different forms of incident radiation (a) and with air temperature (b) (12.01.92).

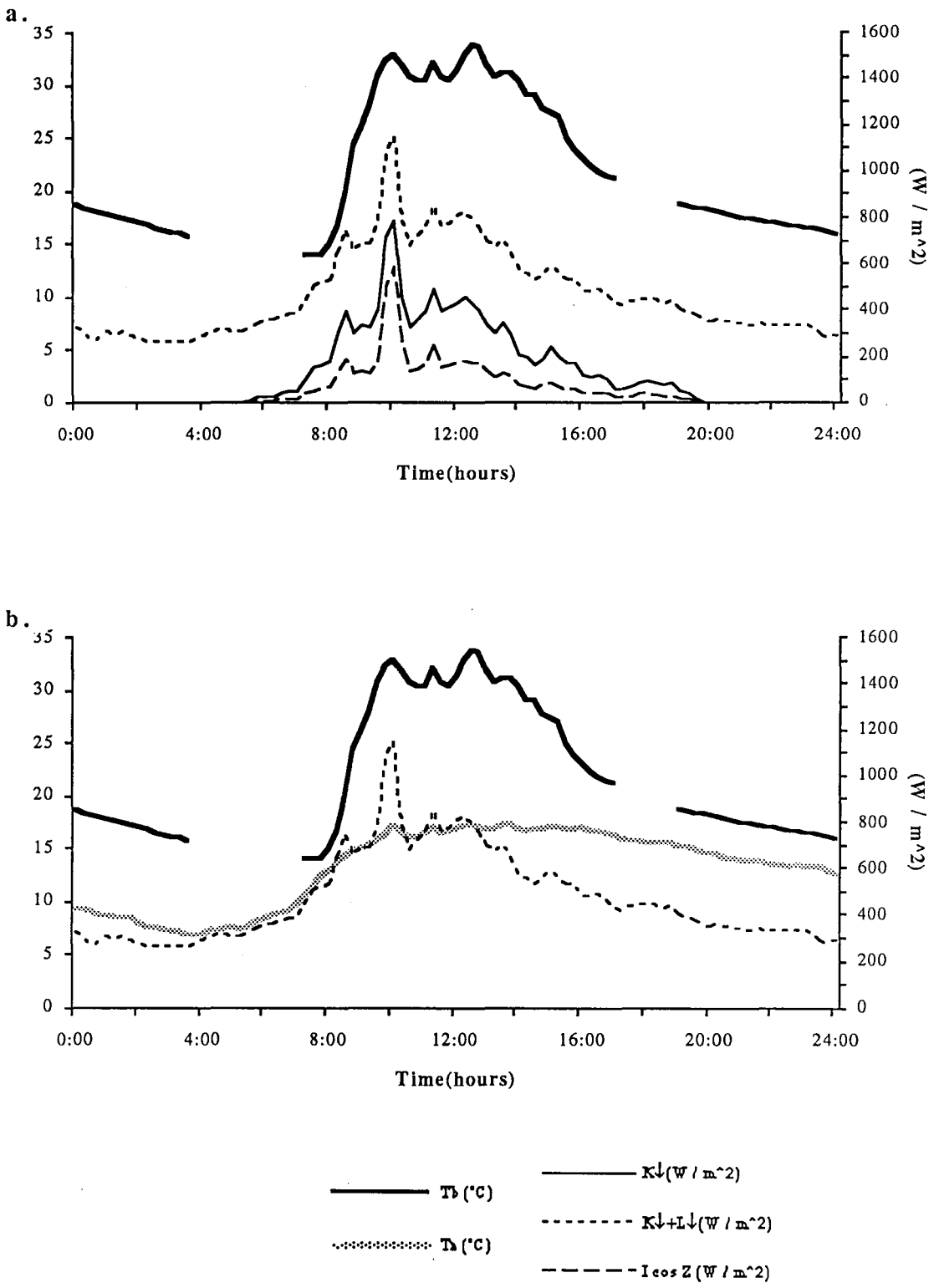


Fig.6.6 Tb profile over 24 hours, with different forms of incident radiation (a) and with air temperature (b) (29.01.92).

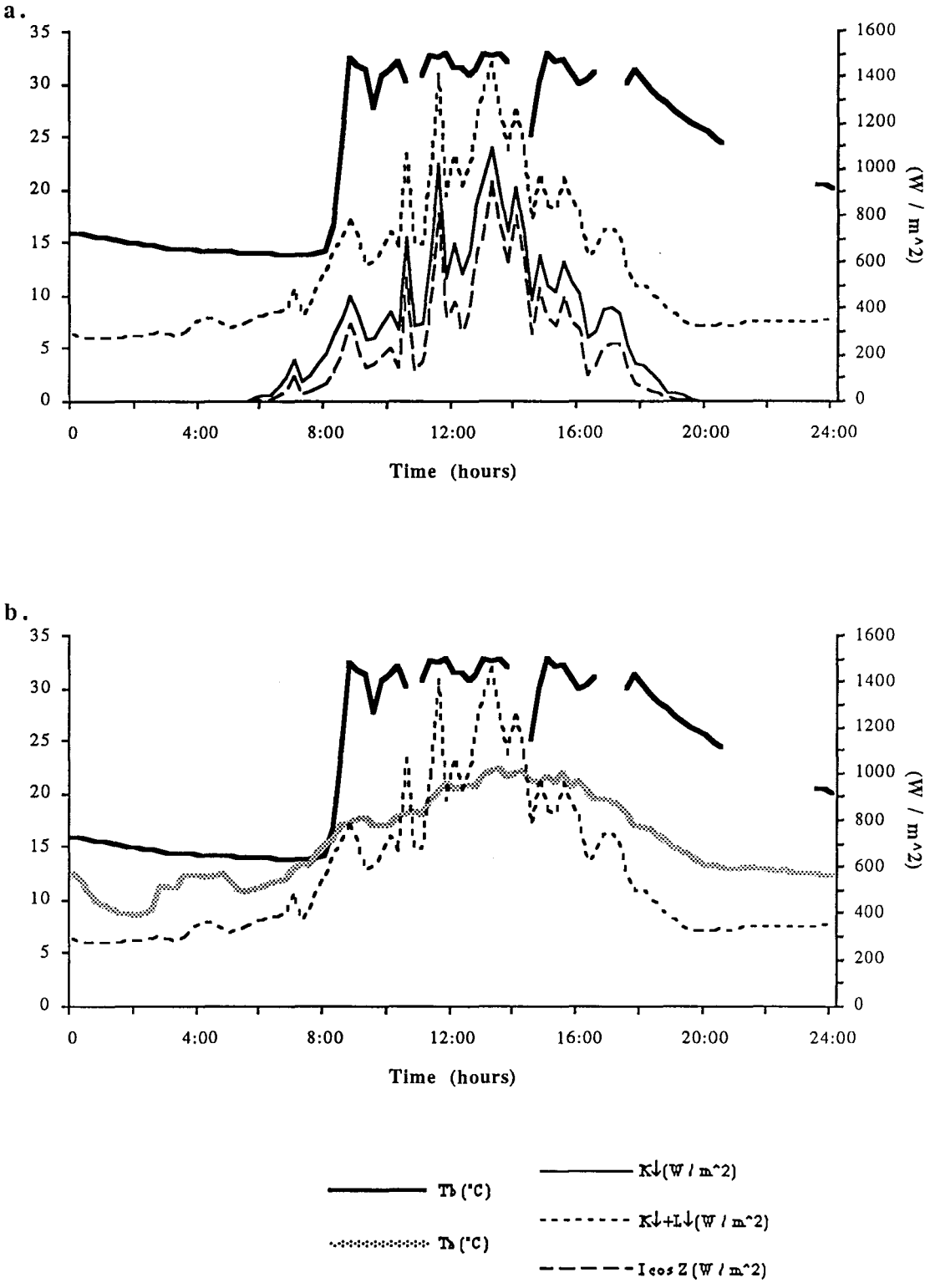


Fig.6.7 Tb profile over 24 hours, with different forms of incident radiation (a) and with air temperature (b) (30.01.92).

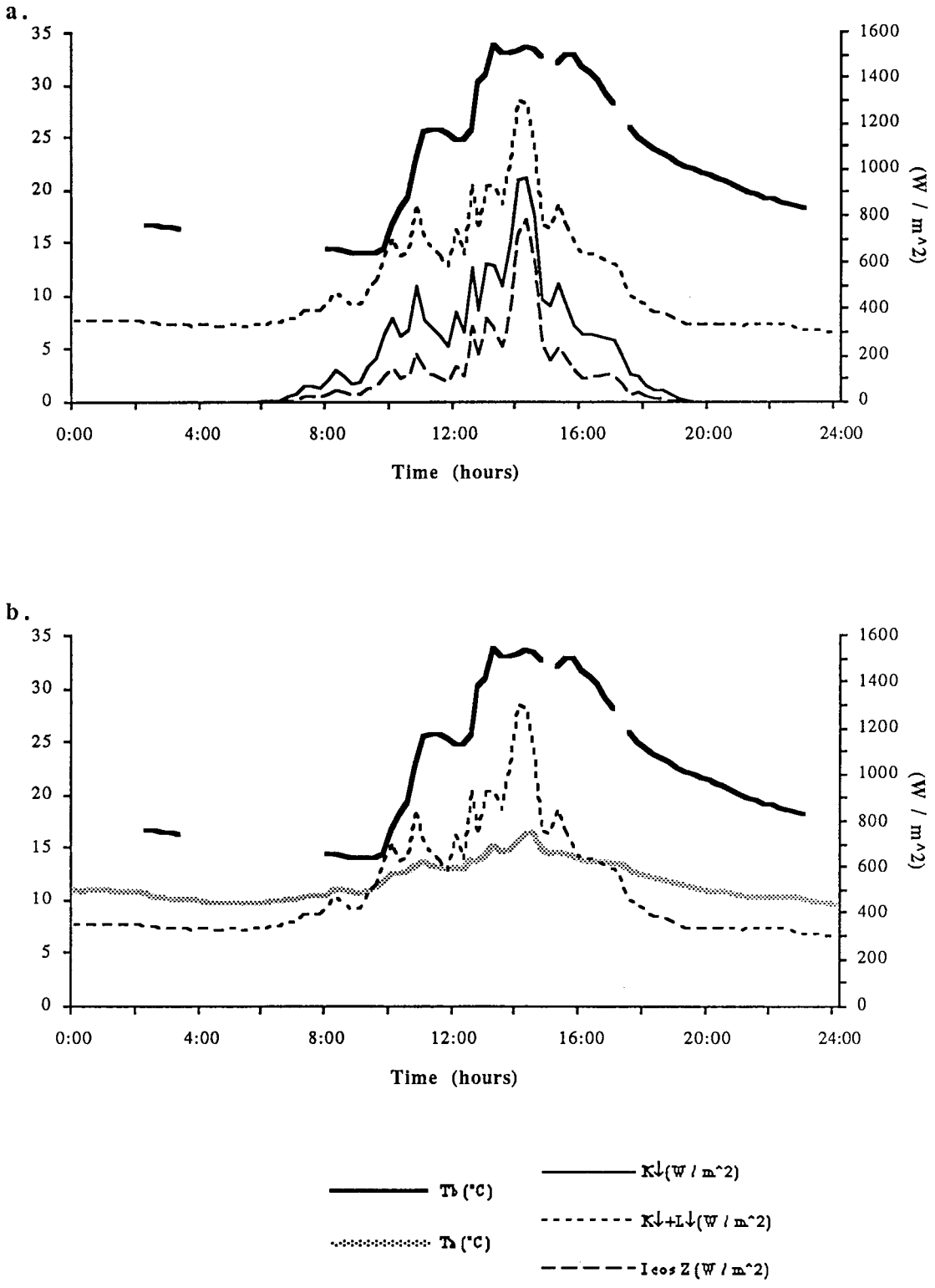


Fig.6.8 Tb profile over 24 hours, with different forms of incident radiation (a) and with air temperature (b) (14.02.92).

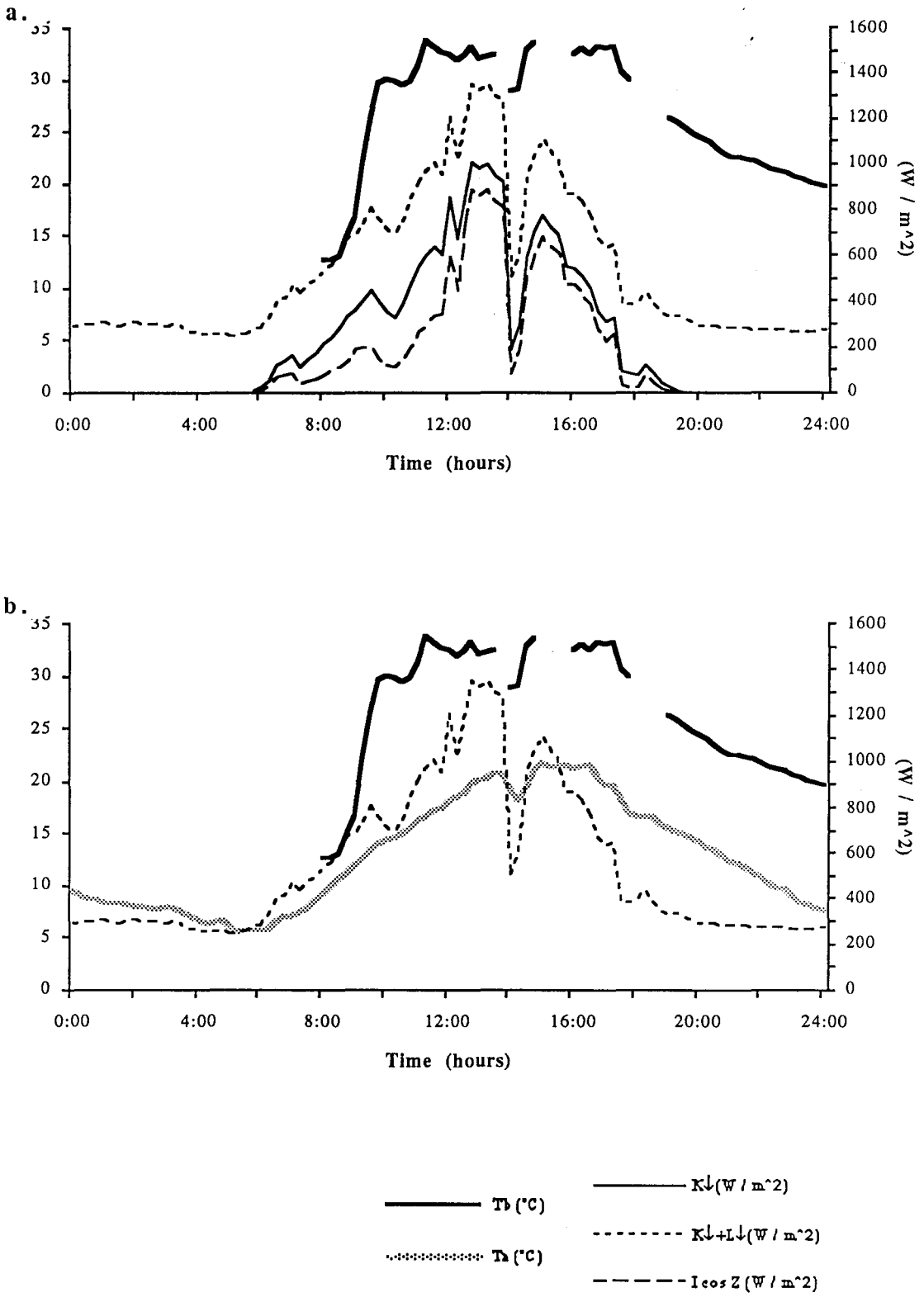


Fig.6.9 Tb profile over 24 hours, with different forms of incident radiation (a) and with air temperature (b) (15.02.92).

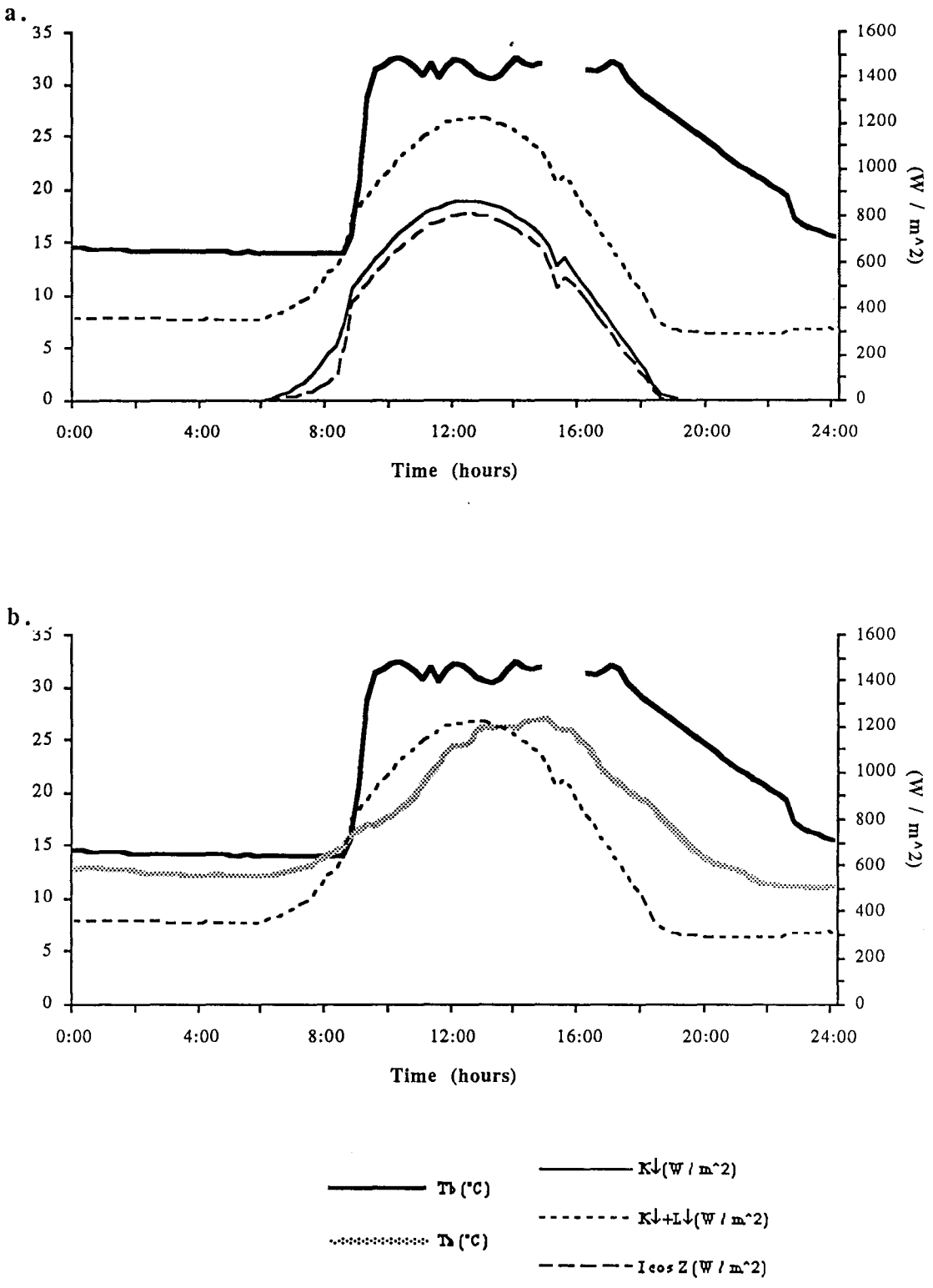


Fig.6.10 Tb profile over 24 hours, with different forms of incident radiation (a) and with air temperature (b) (28.02.92).

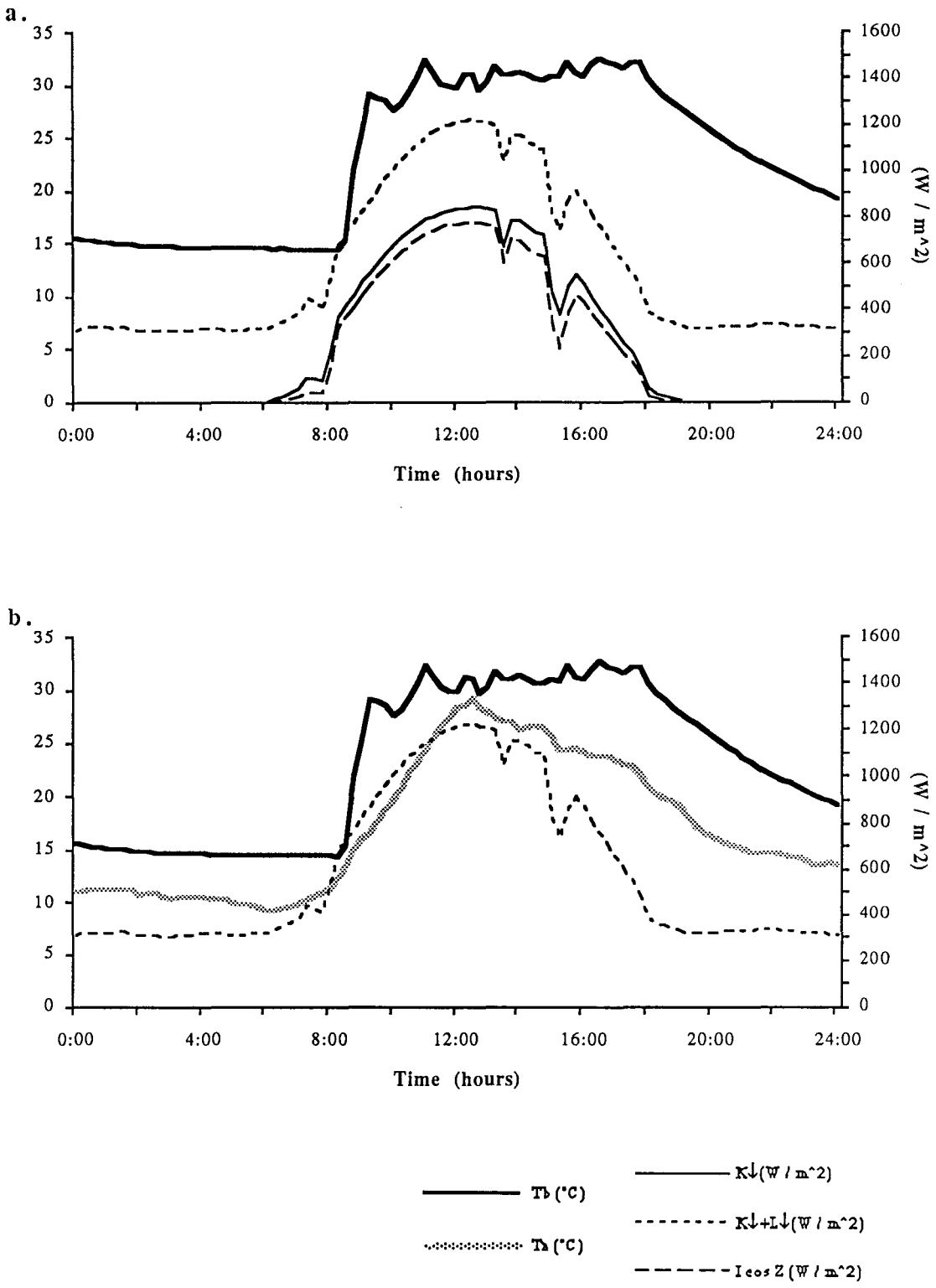


Fig.6.11 Tb profile over 24 hours, with different forms of incident radiation (a) and with air temperature (b) (29.02.92).

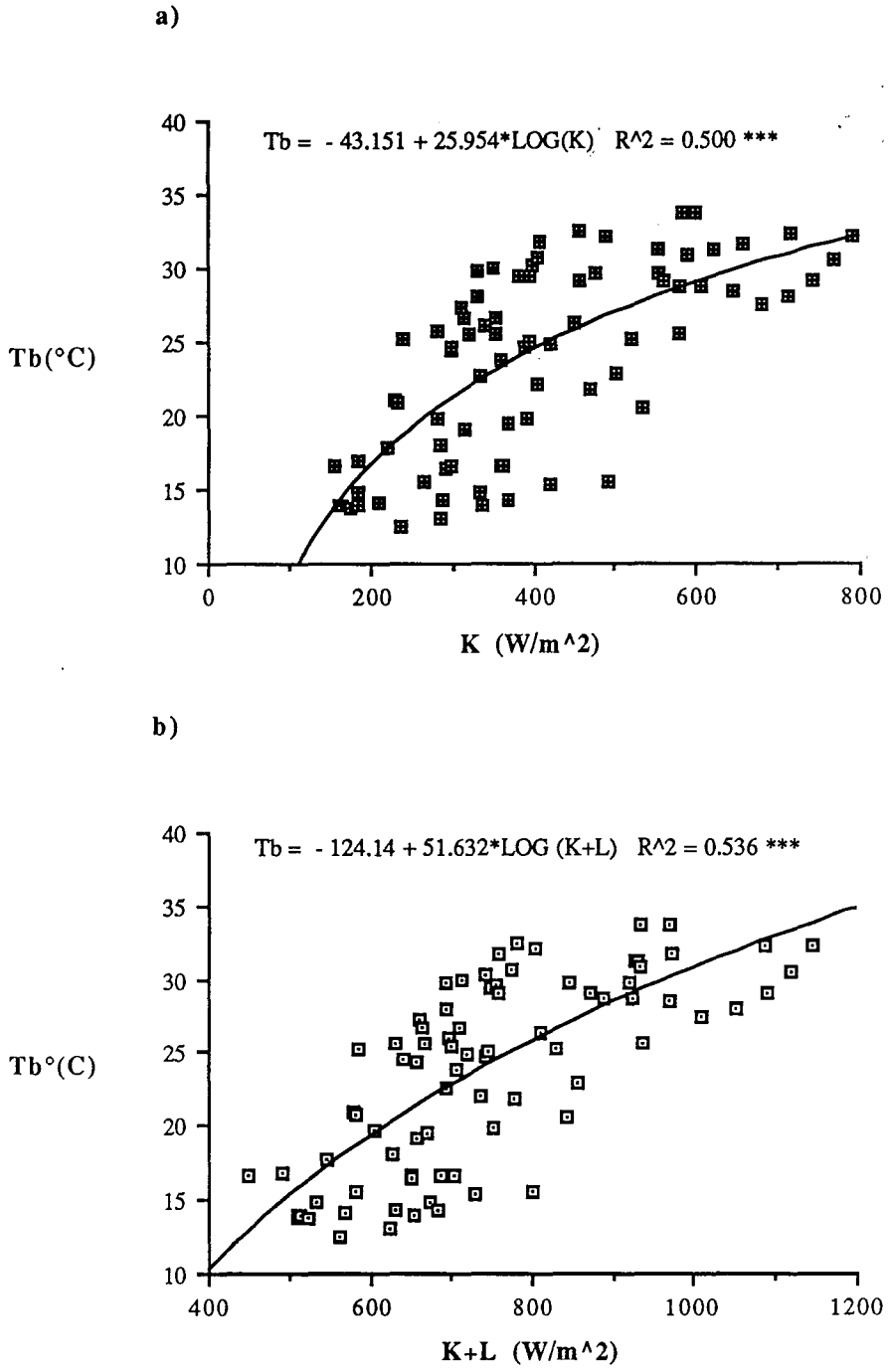


Fig.6.12 Correlations of incoming radiation with Tb, showing the grouped data sets for K↓ (a) and for K↓+L↓ (b)

Despite the apparent strength of the combined radiation index (K↓+L↓) for predicting Tb, the data for individual days, under similar conditions and rates of Tb increase, show K↓ will on occasion be the stronger predictor. This occurred between the two Egg Island sub-sites during clear-sky periods where snakes generally bask on grass pads at S1 and on bracken litter/earth pads at S2. Figure 6.13a shows K↓+L↓ to be

the stronger on S1 (earthen pad, 11.01.92) while K↓ is the stronger on S2 (grass pad, 30.01.92) under similar conditions (Fig.6.13b).

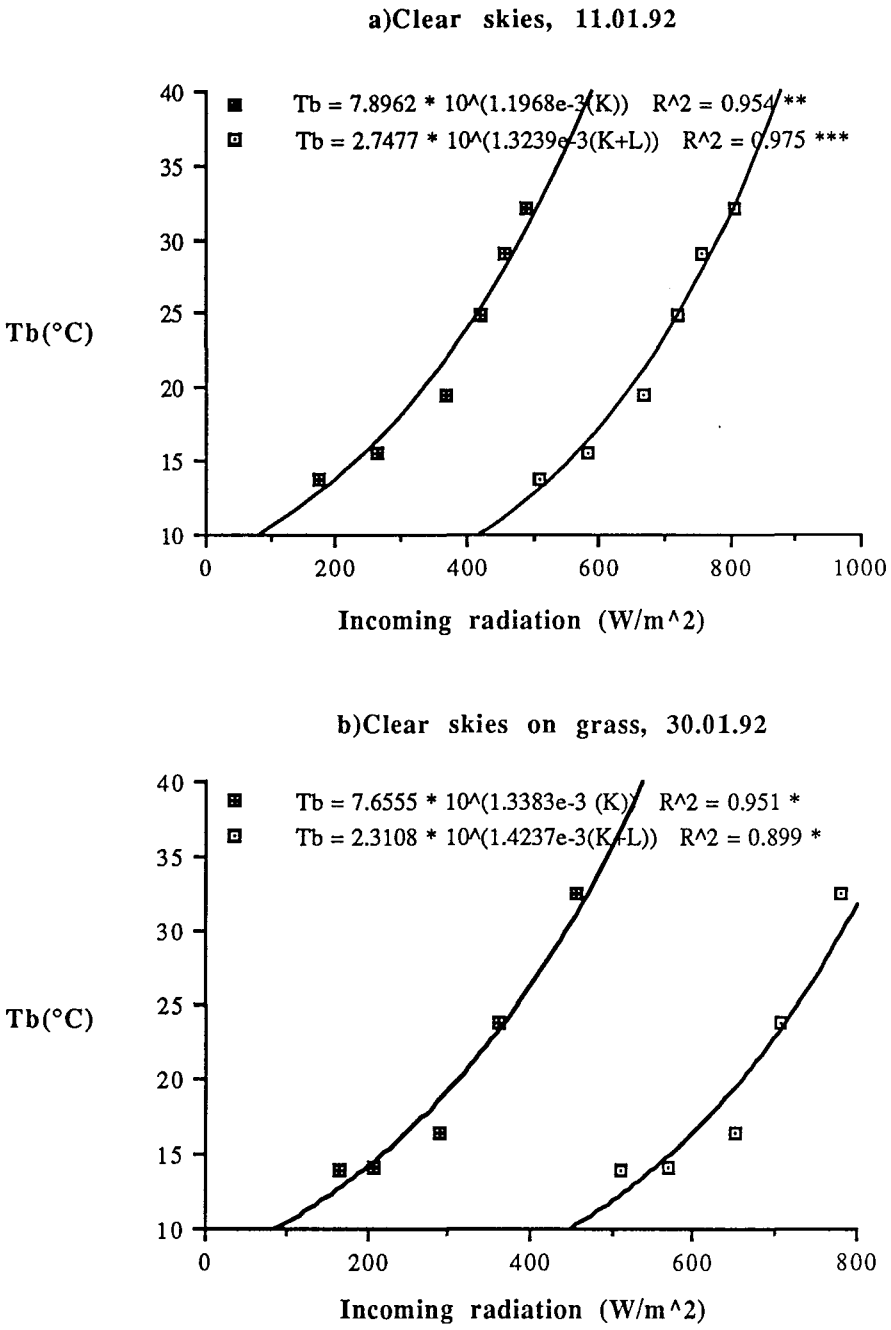
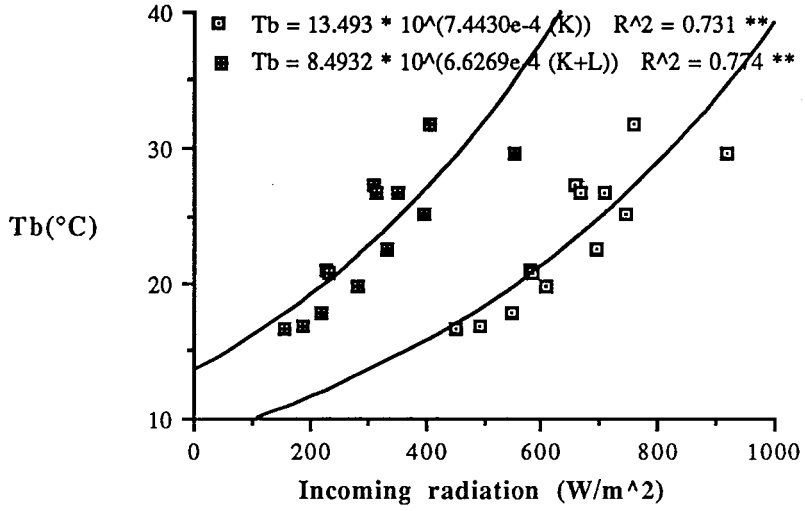


Fig. 6.13 Correlations of incoming radiation K↓+L↓ and K↓with Tb, showing the strength of the relationships for earthen pads (a) and for grass pads (b)

On overcast days both radiation indices were weaker predictors of Tb at both sub-sites (Fig.6.14a and b), and during periods of persistent rain both became unreliable as an index of Tb, giving similar results (Fig.6.15). The results of the correlations with equations for lines of best fit are shown in Table 6.3.

a.



b.

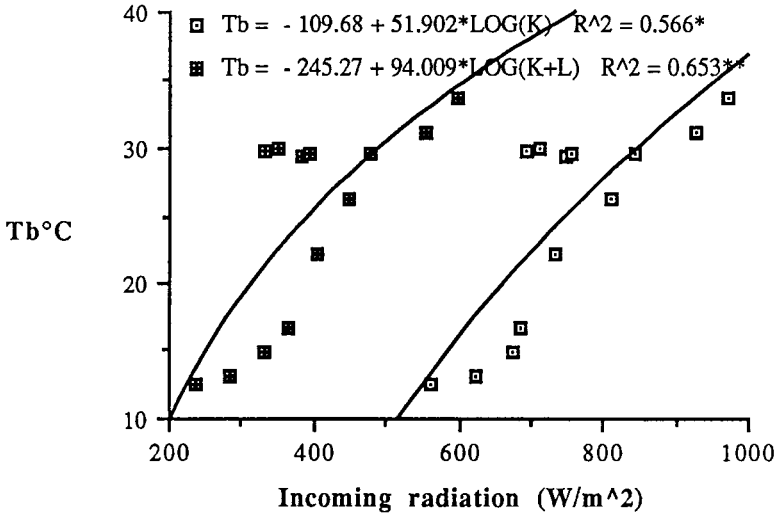


Fig. 6.14. Correlations of incoming radiation K↓+L↓ and K↓with Tb on cloudy days, showing the strength of the relationship for earthen pads (a) and for grass pads(b)

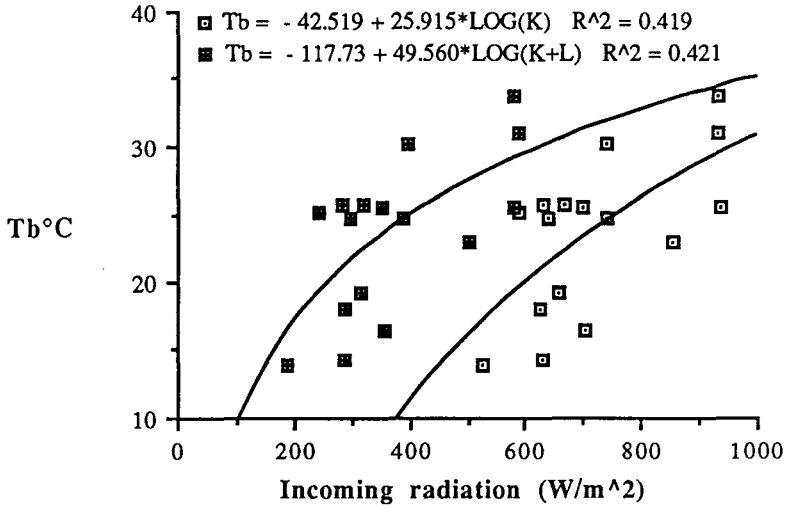


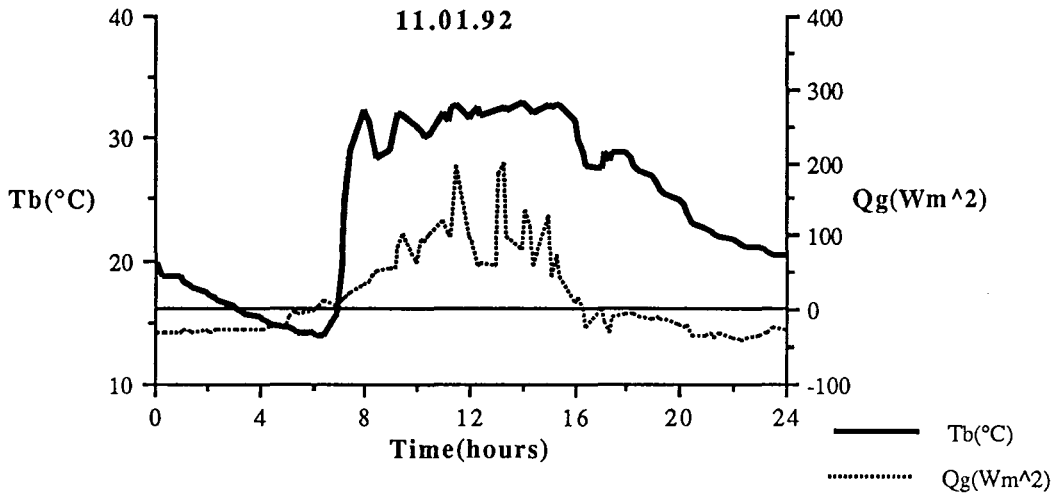
Fig. 6.15. Correlations of incoming radiation K↓+L↓ and K↓with Tb on rain days

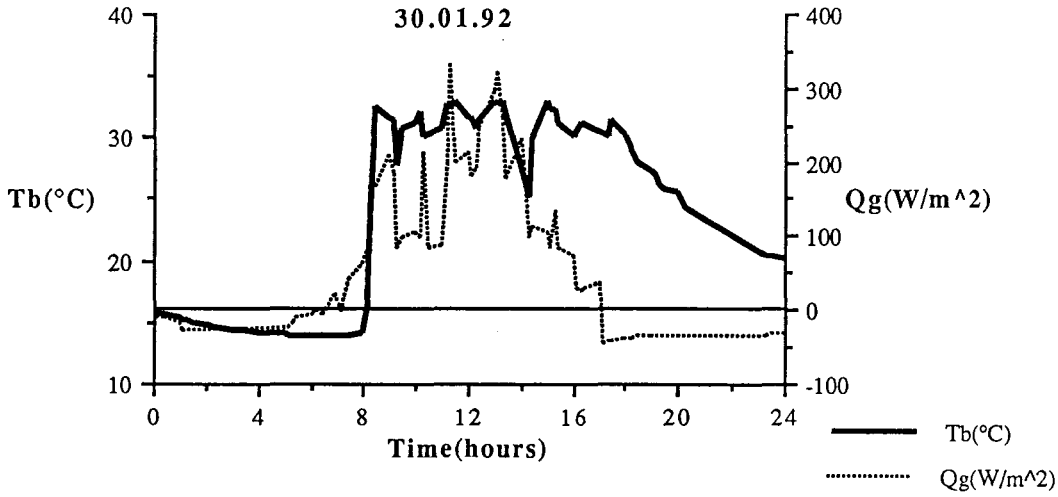
Table 6.3 Correlations of Tb with K↓ and K↓+L↓

TEST GROUP	EQUATION (TB=)	r^2	r	n-2
COMBINED	Tb=-43.151+25.954*LOG(K↓)	0.500	0.707***	78
COMBINED	Tb=-124+51.632*LOG (K↓+L↓)	0.536	0.732***	78
CLEAR S1	Tb=7.8962*10^(1.1968e-3(K↓))	0.954	0.977**	4
CLEAR S1	Tb=2.7477*10^(1.3239e-3(K+L))	0.975	0.987***	4
CLEAR S2	Tb=7.6555*10^(1.3383e-3(K))	0.951	0.975*	4
CLEAR S2	Tb=2.3108*10^(1.4237e-3(K+L))	0.899	0.948*	4
CLOUD S1	Tb=13.493*10^(7.4430e-4(K))	0.731	0.855**	11
CLOUD S1	Tb=8.4932*10^(6.6269e-4(K+L))	0.774	0.880**	11
CLOUD S2	Tb=-109.68+51.902*LOG(K)	0.566	0.752*	11
CLOUD S2	Tb=-245.27+94.009*LOG(K+L)	0.653	0.808**	11
RAIN	Tb=-42.519+25.915*LOG(K)	0.419	0.647	14
RAIN	Tb=-117.73+49.560*LOG(K+L)	0.421	0.649	14

significance level: * = P≤0.05, ** = P≤0.02, *** = P≤0.01

When both radiation indices are plotted against Tb they suggest the quantity of radiant energy required to elevate snake Tb to eccritic levels and these empirical relationships are detailed in Section 7.1; however, these relationships pertain only to non-gravid animals. Note that Tb rates plateau for a period at similar quantities of K↓ with both cloud and rain (Fig.s 6.14-15).





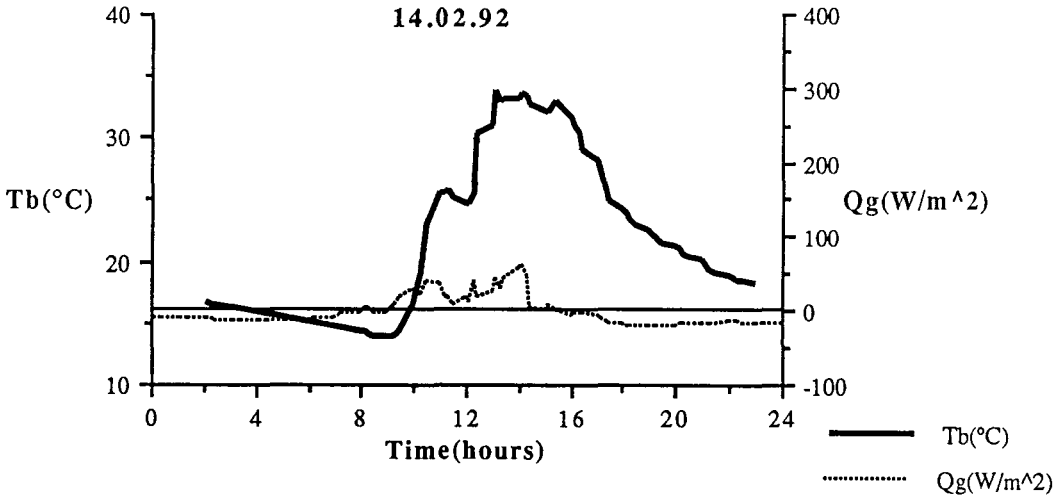


Fig. 6.16. Continued over

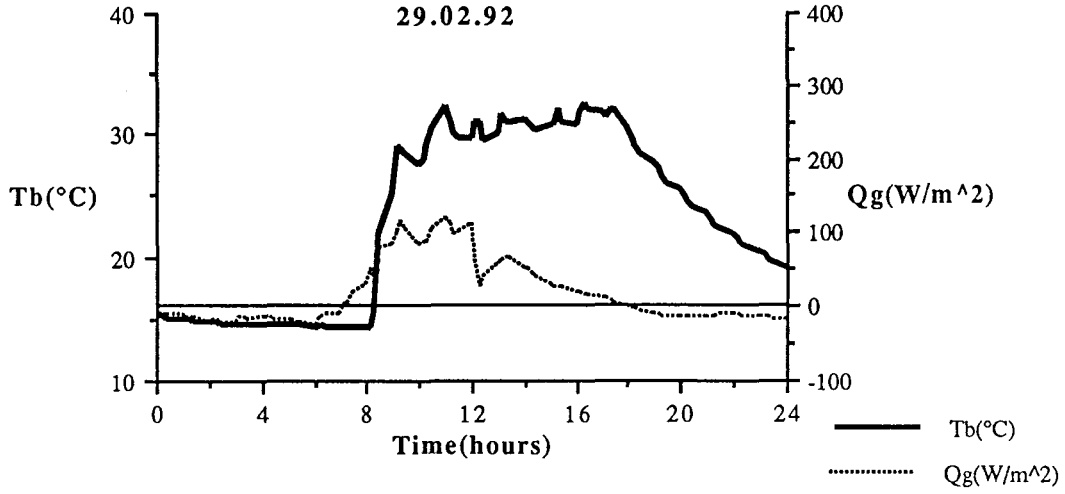


Fig.6.16. Q_g and Tb over 24 hours, showing the relationship of between Q_g and emergence

6.4.2 Ground heat-flux

Accurate interpretation of ground heat-flux (Q_g) in the immediate vicinity of the animal was relatively difficult to determine due to the high degree of ground surface heterogeneity at some of the basking-sites used and because of movement by the animals. Nonetheless, Q_g was found to be a reliable indicator of when snakes would enter night-time retreats in situations where animals were on the ground surface, but it was not as reliable in situations where snakes were on tussock grass pads (the usual situation at S2). The dependence of Q_g's on sky-view factor, even between small tussocks, meant that a lag occurred at S2 from the time Q_g became negative and the time snakes entered their retreats (Table 6.4, Fig.6.16: 30.01.92 and 14.02.92). In addition, snakes on grass tussocks had more radiant opportunity, when the sun was low, as they were largely independent of ground surface aspect (unlike the snakes at S1) and the elevation allowed them access to the last of the sun's rays. Conversely, the entry into night-time retreats of those snakes which usually basked on the ground surface in the late afternoon (S1) coincided closely with Q_g as it approached zero (Fig.6.16: 11.01.92 and 29.02.92). This occurred even in low radiant energy situations.

The data suggest that the female snakes at Egg Island are maximising their thermal opportunities in the late afternoon by delaying entry into night-time retreats until there is no more incoming radiant energy; however, Tb would usually be decreasing at this stage and entry become increasingly more likely as Tb approached or dropped below 30°C. Entry was often triggered by a cloud passing over the sun or a small gust of wind, both of which were shown by the telemetry to result in a rapid increase in heat

loss at this time of day.

Contrary to the above, Q_g could not be related to emergence, as it became positive in the early morning, and snakes would often emerge from night-time retreats more than a hour later.

Table 6.4 Q_g and time of entry into night-time retreats

DATE	TYPE OF PAD	TIME OF ENTRY	$Q_G(Wm^{-2})$
10.01.92	EARTH/BRACKEN LITTER	18:31	0.3
11.01.92		18:00	0.6
12.01.92		18:01	3.5
27.02.92		17:45	-0.1
28.02.92		17:15	2.9
29.02.92		17:51	0.1
28.01.92**	GRASSES	18:36	7.04
29.01.92		16:45	-4.0
30.01.92		17:40	-29.0
13.02.92**		15:53	-20.1
14.02.92		16:10	-15.6
15.02.92		17:13	-8.25

** Rain

6.4.3 Cloud

Cloud occurred on most days and influenced both the quality and quantity of incoming radiation. Cloud-cover was in excess of 80% on 75% of telemetry study days and cloud-effects depended on both the type and height of cloud. Generally, these effects are indicated in plots as sharp spikes in incoming radiation (Figures 6.4a-11a). However, the radiation plots represent fifteen minute mean values only, while cloud effect is almost instantaneous, and breaks in cloud-cover can result in relatively rapid rates of Tb increase (e.g. 0.5°C $minute^{-1}$) which might be masked by the method of sampling used. The influence of cloud on Tb is well illustrated in Fig.6.6a where the snake in this case is fully exposed to the sky and waits for long periods between cloud-breaks, represented as sharp peaks in the plots of incoming radiation.

The effects on Tb seen in Table 6.5 are not solely due to cloud cover. Nonetheless, as cloud influences the available radiant energy (i.e. solar and thermal radiation) it

can be seen in Table 6.5 to have a profound effect on Tb and consequently on Tiger Snake behaviour. This contrasts with the findings of Dredge (1981) and is discussed further in Section 7.4.

Table 6.5 Days where cloud cover was ≥90%, during morning basking periods, and the effect on Tiger Snake Tb

DATE	CLOUD(c)%	EFFECT (OBSERVED) ON Tb
10 Jan.	c=90	lag then steep increase
12 Jan.	c >90	slow increase, goes backward, eccritic at 11 a.m.
28 Jan.	c ≈ 90	slow increase, eccritic at 10:15 a.m.
29 Jan.	c >90	slow increase, Tb goes backwards
13 Feb.	c = 100	very slow increase
14 Feb.	c =90	starts slow, Tb plateau at ≈25°C, enters early
15 Feb.	c ≈90	steep increase, Tb plateau at ≈29°C, eccritic at 11:00 a.m.

6.5 PRECIPITATION

Contrary to widely held belief, Tiger Snakes are active in the rain (in summer) and so rainfall can influence their thermoregulatory behaviour. For this reason rainfall has been included in the results.

Rainfall data (mm) are shown separately for overnight (0700-1900 hours) and daytime (1900-0700 hours) periods in Table 6.6. Rainfall data (0900 to 0900 hours, Bureau of Meteorology) for Huonville (6.5km NNE) are included for regional comparison.

Table 6.6 shows the percentage of the Egg Island females found to be above ground in exposed positions during rain periods. All females studied were observed on or near basking pads during rainfall on at least one occasion and two of the seven females were on basking pads on every one of the rain days. Although snakes emerged on days with light showers they usually did so later than on fine days as evident on the Tb profiles (Fig.6.8). If rain or thick cloud prevented them from reaching eccritic temperatures until late in the day or if they experienced steep drops in Tb, they often entered night-time retreats earlier than usual in mid afternoon (Fig.6.8).

The precipitation data further supports the hypothesis that Tiger Snakes will attempt to maximise their thermal opportunity at sea-level in Tasmania and will attempt to increase their Tb's even on wet days in summer. Snakes that are above ground at such times may not be visible to the casual observer as they often utilise available

ground cover and may only become visible between showers. Not all of the population will be above ground however, as is evident from Table 6.6.

The above behaviour was not found to be the case at Lake Crescent, possibly due to lower environmental temperature, and no snakes were observed in rain above 800m. Snakes were observed, however, to attempt to bask between showers at Clarence Lagoon (1000m) during February.

Table 6.6 Rainfall data (mm) and percentage of the adult female population observed on or near basking pads

DATE	OVERNIGHT	0700-1900 HOURS	HUONVILLE	% BASKING
27.12.91	0	0.1	0.4	71
28.12.91	0	1.1	0	43
08.01.92	0	0.1	0	57
11.01.92*	0	0.1	0.4	43
26.01.92	1.6	0.1	0.2	71
27.01.92	0	0.4	1.0	57
28.01.92*	2.1	0.1	0.6	71
29.01.92*	0.3	0.3	0	57
31.01.92	0	0.1	0	57
10.02.92	0.1	0.1	0.4	57
11.02.92	0	6.7	8.0	43
12.02.92	1.6	0.1	0.2	43
13.02.92*	0.1	0.2	2.0	43

* Telemetry study days used in the discussion

6.6 TEMPERATURE

6.6.1 Ground surface temperature

Mean ground surface temperature (T_r) differences, in one metre quadrats for the Egg Island female home-sites, are presented in Fig.6.17a, b. The data used to compile the thermal maps were taken within four days of completion of the telemetry studies and are representative of mean T_r differences occurring in each home-site on a typical and partly cloudy day. Each of the maps in Fig.6.17 contain the combined home-sites of two animals. They show the relative positions of the burrows (night-time retreats) and all basking pads; the use of the pads varying with time of day and weather. The data show these locations to have usually been the warmest ground surfaces available

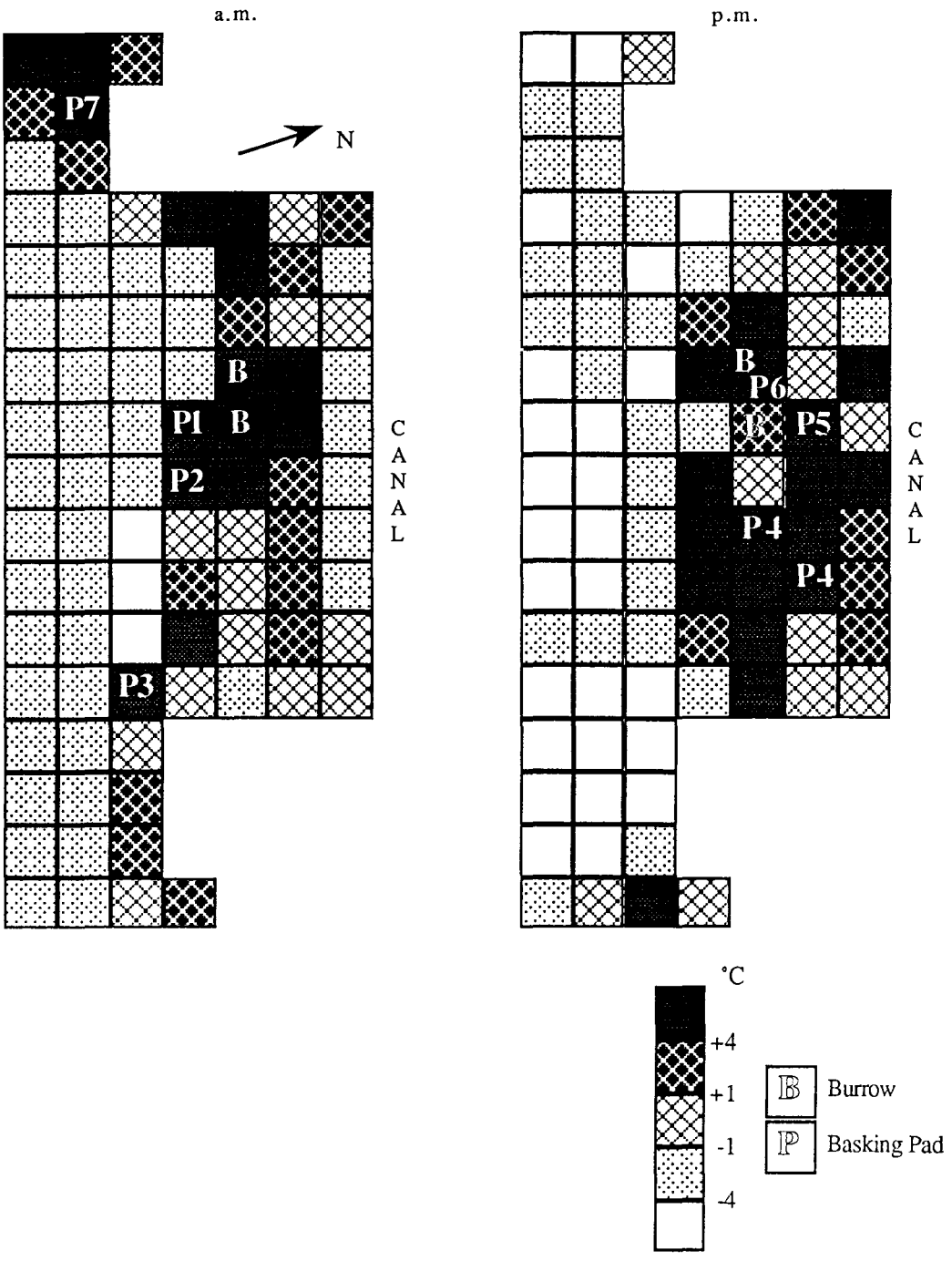


Fig. 6.17 a Deviation from the mean ground surface temperature(°C) in one metre quadrats at the Egg Island Sub-site 1.

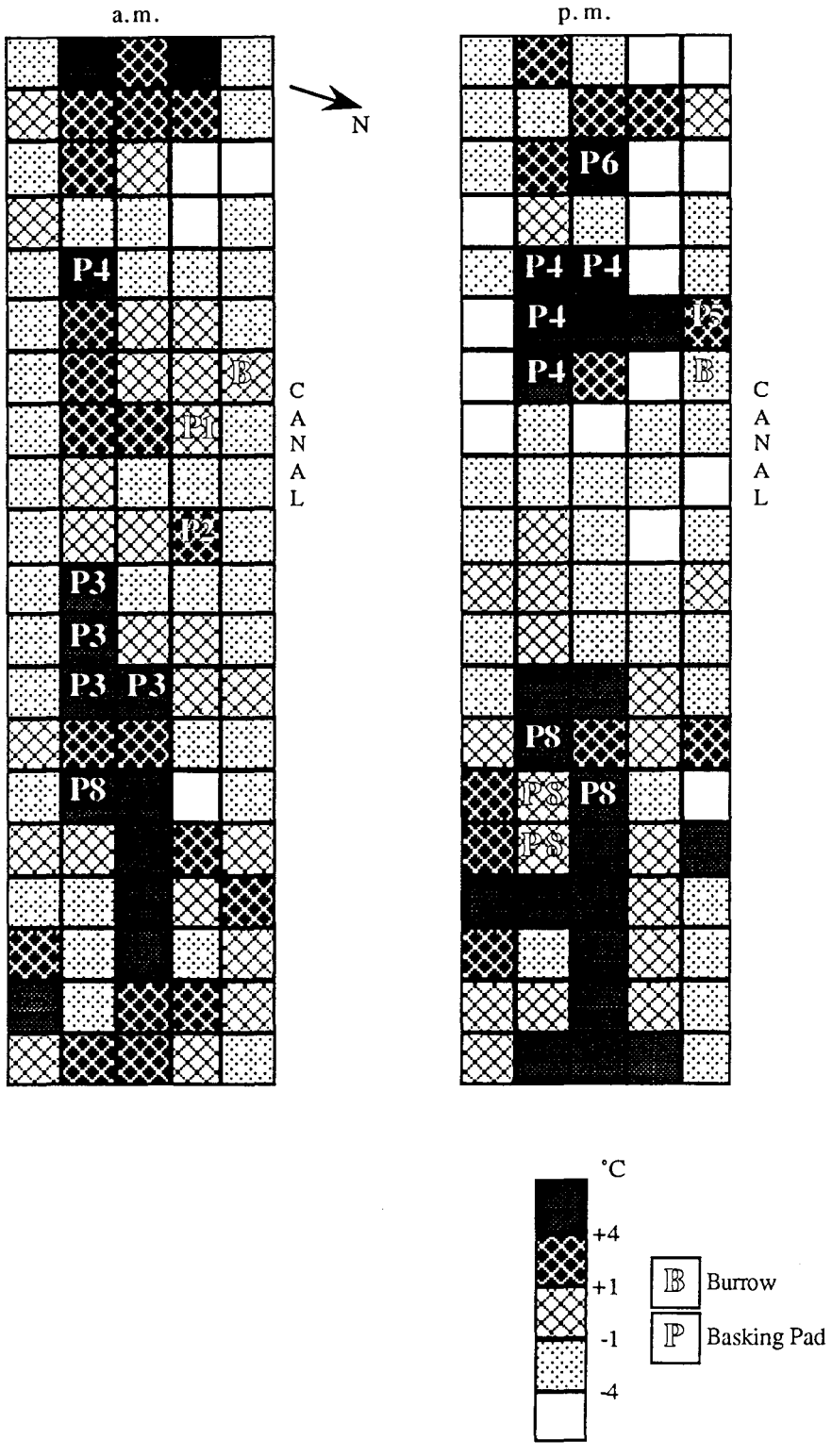


Fig.6.17 **b** Deviation from the mean ground surface temperature(°C) in one metre quadrats at the Egg Island Sub-site 2

to the snakes in early morning and late afternoon, and pad choice by the snake was always wind dependent. However, early morning pads next to night-time retreats were usually cooler than the mean basking-site temperatures and were used only briefly until such time as the animals had warmed sufficiently before moving to the more suitable sites (usually at Tb>18°C). Snakes would often undergo this initial warming phase with part of their bodies still inside the night-time retreats. On cold days with a southerly wind and/or thick cloud all snakes would remain within one metre of night-time retreats for long periods, often for several hours.
The Lake Crescent basking pads and those of most of the other snakes observed above 800m were found to be approximately located within one metre of the entrance to night-time retreats (94.1%, n =17) and, unlike the basking pads most often used by the Egg Island animals, these were often the only pads the higher elevation snakes were observed to use.

The Tb's and pad T_r's for eight-one hour basking periods are presented in Table 6.7. Simple correlations were performed on all fifteen minute mean T_r and Tb values which gave variances of: 0.606 (n-2=48) for the grouped data, and 0.672 (n-2=38) for the non-gravid female data; both of these show highly significant relationships ($P<0.001$) between pad T_r's and Tb's. The strength of this relationship is not surprising for an ectotherm in close contact with the ground surface. The closer relationship between T_r and Tb for non-gravid females is explained by the basking behaviour of the gravid female (during the ten weeks of observations) which moved onto early morning pads later than the non-gravid females and avoided the hotter bare earth surfaces, thus purposely slowing her rate of Tb increase by moving off pads while still several degrees below her mean eccritic temperature (Table 6.1, Fig.6.11).

The method of measuring pad T_r's would have resulted in unknown sampling errors, especially on grass pad surfaces, as these could not be measured directly without disturbing the animals. T_r of telemetered animal pads was inferred from mean surface temperature differences and through interpolating between pre-basking and post-basking values. The importance of surface temperatures to the thermal ecology of these animals warrants a more detailed measurement technique than was possible here.

It was often possible to predict the movement or location of animals by surface temperature differences alone. For example, no snakes were ever found on T_r's greater than 35°C which meant that animals would not be found on solar exposed earthen surfaces for the larger part of sunny days as they spent most of such days on or under the cooler grasses or secreted in the marsh area. The exact location of

day-time retreats varied with wind direction. This situation was the reverse in early morning and late afternoon; however, on overcast days, animals generally spent relatively longer periods on the warmest suitable surfaces available. Generally, animals were often easy to find until T_r's approximated their mean eccritic temperatures and thereafter finding them became progressively more difficult until searching for them became pointless (i.e. on T_r's >35°C). Nonetheless, each animal could be relied upon to reappear again onto afternoon pads as surface temperatures dropped below 35°C.

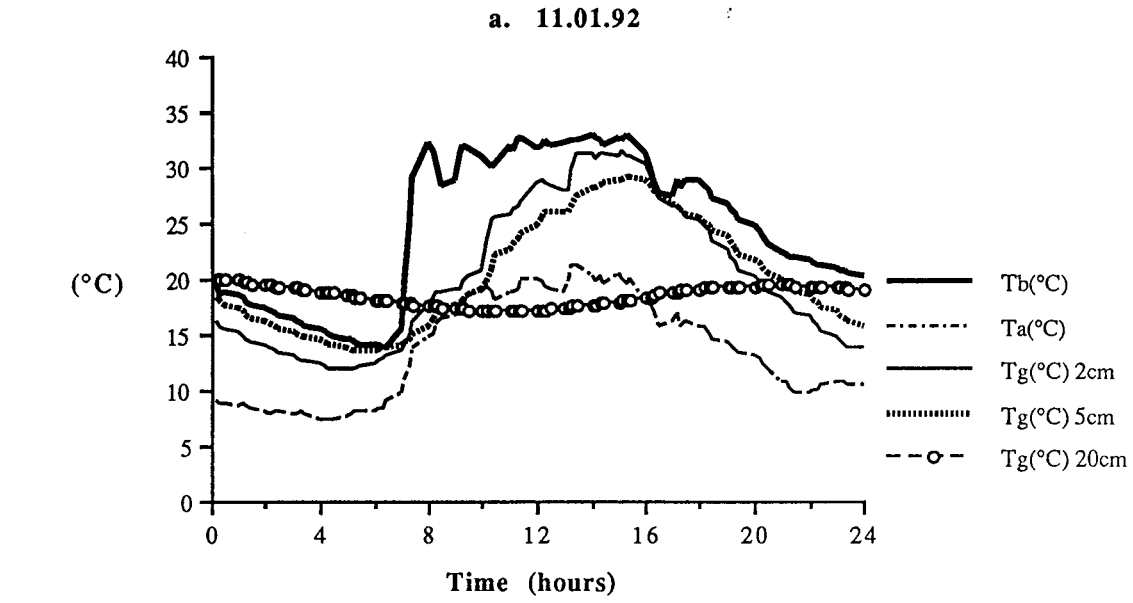
Table 6.7 Emergence times, pad surface temperature (T_r) and body temperature (Tb) relationships during one hour basking periods on two consecutive days for each animal

DATE	ANIMAL/SUB-SITE	EMERGED	TIME	PAD T_r(°C)	Tb(°C)
10.01.92	A1/S1**	07:22	07:30	15.5	15.69
			08:30	19.5	20.337
11.01.92	A1/S1**	06:45	07:00	13.5	15.56
			08:00	28.0	32.18
29.01.92	A2/S2++	07:33	07:45	14.1	14.01
			08:45	16.4	24.39
30.01.92	A2/S2++	07:42	07:45	17.3	13.87
			08:45	23.7	32.5
14.02.92	B2/S2++	09:30	09:30	12.5	13.86
			10:30	15.5	19.14
15.02.92	B2/S2++	08:50	09:00	13.5	16.62
			10:00	24.0	29.95
28.02.92	*C1/S1**	08:30	08:30	24.1	13.93
			09:30	32.5	31.2
29.02.92	*C1/S1**	08:17	08:30	17.0	15.32
			09:30	31.8	28.68

*gravid female, ++ grass pads, ** earth and litter pads

6.6.2 Inground temperature

Fifteen minute mean inground temperatures (T_g's) are compared with Tb and air temperature (T_a) profiles in Figures 6.18a-21a. Rank correlations were obtained for the grouped data which showed T_g at five centimetre depth to have a strong relationship with Tb (r^2 = 0.757, n = 788, P<0.001); however, T_g at two centimetres showed a stronger relationship (r^2 =0.865) and T_g at twenty centimetres showed no significant relationship (r^2 = -0.28). The strength of the relationship between T_g(2cm) and Tb is readily understandable as this variable tracks ground surface temperature which strongly influences Tb during daylight hours (Section 6.6.1). The poor correlation between T_g(20cm) and Tb suggests the animals do not usually retreat to this depth in the soil.



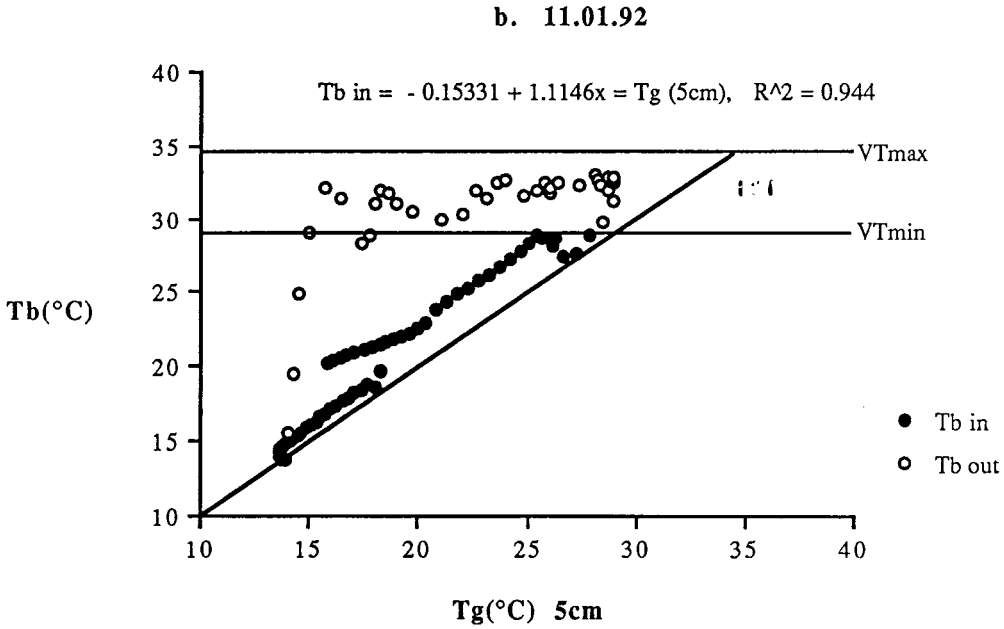


Fig.6.18 11.01.92 a) Temperature regime over 24 hours. b) Climate space using Tg (5cm) over 24 hours

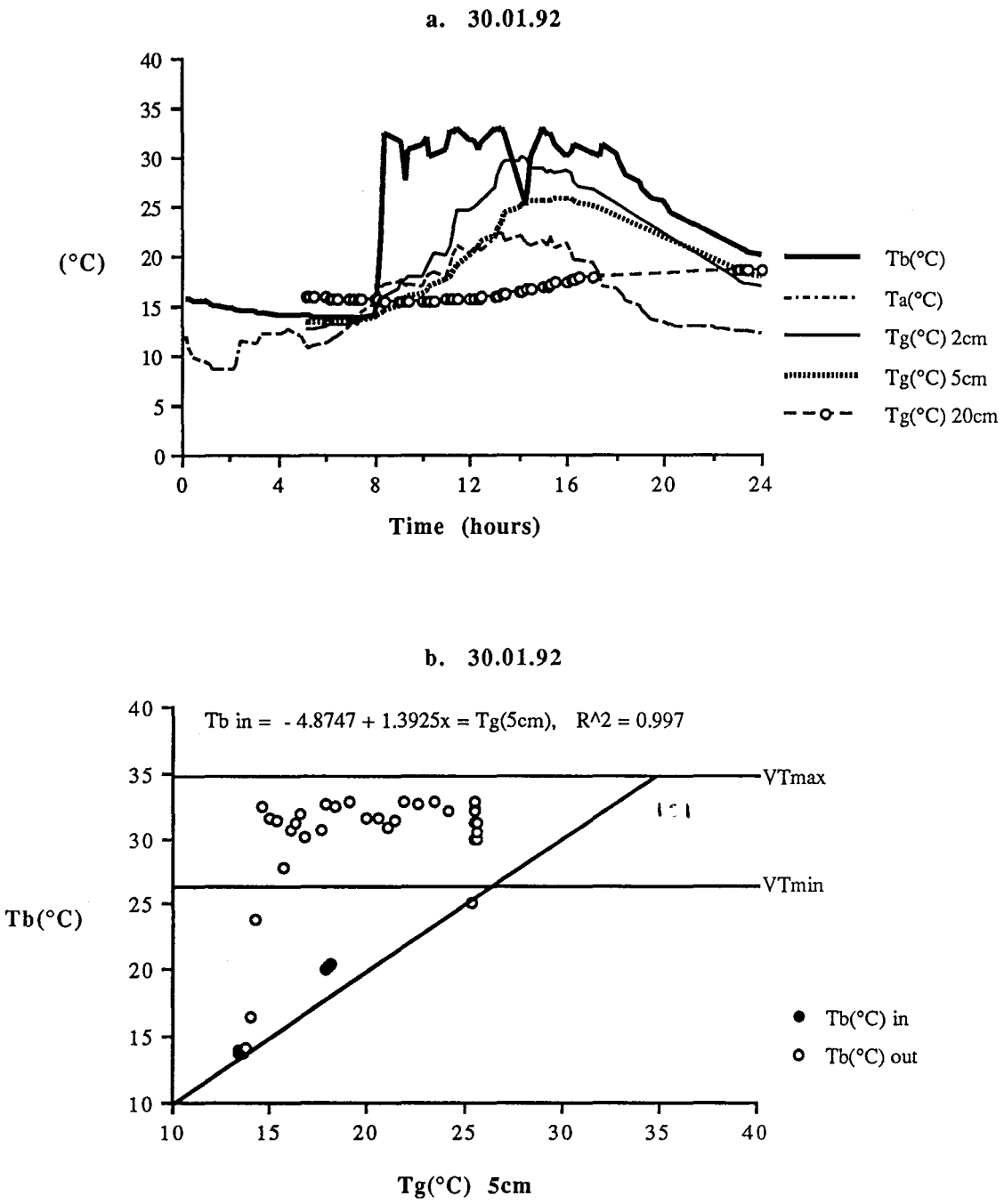
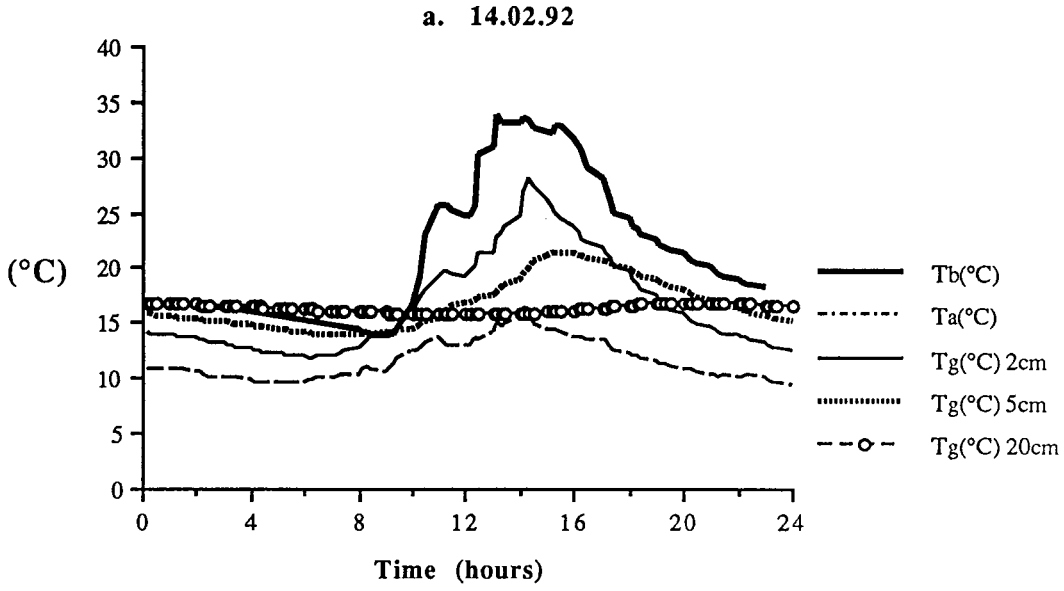


Fig.6.19 30.01.92 a) Temperature regime over 24 hours. b) Climate space using Tg (5cm) over 24 hours



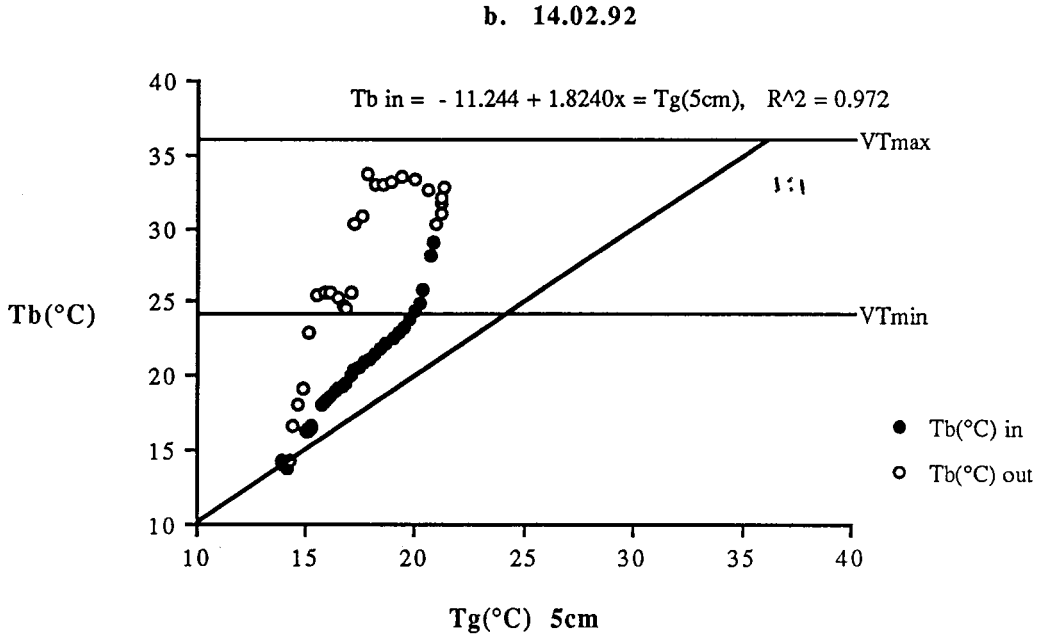


Fig.6.20 14.02.92 a) Temperature regime over 24 hours. b) Climate space using Tg (5cm) over 24 hours

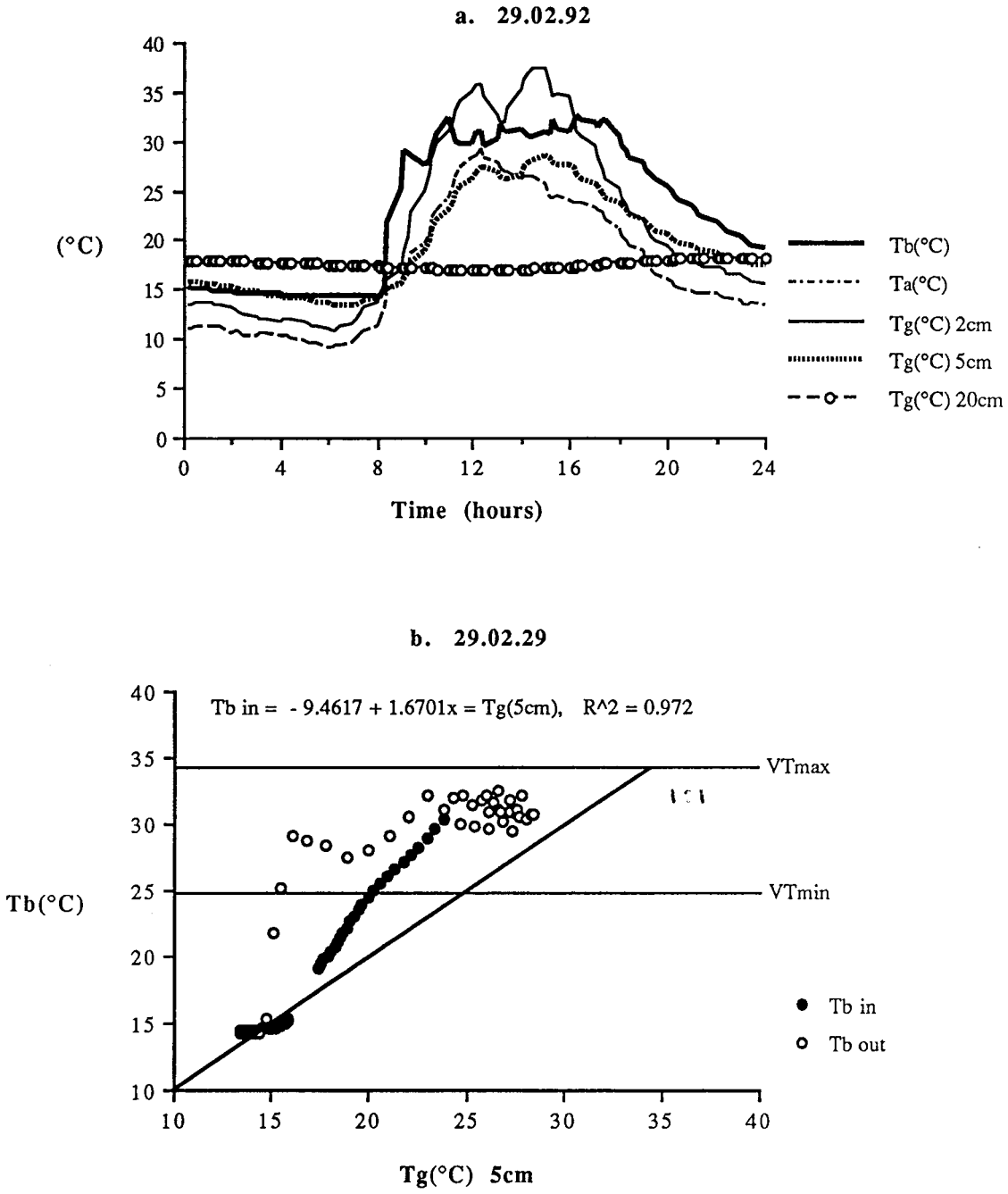


Fig.6.21 29.02.92 a) Temperature regime over 24 hours. b) Climate space using Tg (5cm) over 24 hours

The strength of the relationship between T_g's (5cm) and Tb's varied with ground heat flux and air temperature and is shown for each of the corresponding twenty four hour periods in a modified climate space in Figures 6.18b-21b. The strength of the relationship for when the animals were in and out of night-time retreats was tested for eight days data using Pearson's r correlation coefficient (Table 6.8).

Table 6.8 Correlations (r) of Tb with T_g (5cm) and T_a, for when animals are in and out of night-time retreats

DATE	T_g(5cm)in	T_g(5cm)out	$T_a$in	$T_a$out
11.01.92	0.891***	0.150	0.845***	0.539**
12.01.92	0.929***	0.416***	0.144	0.403***
29.01.92	0.391***	0.010	0.189	0.821***
30.01.92	0.994***	0.066	0.369**	0.261
14.02.92	0.945***	0.493***	0.346*	0.531***
15.02.92	n/a	0.179	n/a	0.432**
28.02.92*	0.895***	0.150	0.319**	0.092
29.02.92*	0.945***	0.326	0.931***	0.326*

significance level: * = P≤0.05, ** = P≤0.02, *** = P≤0.01

The results show a highly significant relationship exists between Tb and T_g(5cm) when animals are inside night-time retreats, however, animals are not always found at this depth throughout the night but at the time of emergence their Tb's often closely correlated with T_g (5cm) (Fig.6.18a-21a).

Animals would occasionally chose to remain just inside burrow entrances, or near the surface and remain visible, on nights when their body temperatures (and thus their body heat stores) were greater than either the air or inground temperature (Fig.6.21a, 6.22). Figure 6.21a shows a plotted Tb of an animal which remained just inside the burrow entrance until just prior to midnight after which she slowly descended. This is indicated by the modified climate space below (Fig.6.21b), where each point on the graph represents the 15 minute mean Tb and which shows this behaviour allows the animal to maintain her Tb within voluntary thermal limits for a relatively long period, and well above T_g(5cm). The point at which animals would descend into burrows appears to be related both to decreasing T_a (e.g. Fig.6.18a, 16:30hrs, where the animal descends and then re-emerges with an increased air temperature at 17:00hrs) and the T_g's (Fig.21a); however, as Tb, T_a and T_g are all responding to incoming radiation (e.g. at approximately 14:00hrs in Fig.6.9) knowledge of this quantity

might in future allow prediction of the behaviour. This relationship could not be further tested here due to the low number of recordings.

Fig.6.22 C1 in her burrow

6.6.3 Air temperature

Air temperatures for each Egg Island female are plotted with Tb and T_g profiles in Figures 6.18a-21a, and rank correlations obtained for the grouped data show a significant relationship with Tb (r^2=0.788, n=899, P=<0.001). The relationship between T_a's and Tb's are shown for each of the corresponding twenty four hour periods in Figures 6.23-24 and the strength of the relationship when the animals were in and out of night-time retreats is shown in Table 6.8.

Emergence from night-time retreats was always associated with increase in T_a (Figures

might in future allow prediction of the behaviour. This relationship could not be further tested here due to the low number of recordings.

Fig.6.22 C1 in her burrow

6.6.3 Air temperature

Air temperatures for each Egg Island female are plotted with Tb and T_g profiles in Figures 6.18a-21a, and rank correlations obtained for the grouped data show a significant relationship with Tb (r^2=0.788, n=899, P=<0.001). The relationship between T_a's and Tb's are shown for each of the corresponding twenty four hour periods in Figures 6.23-24 and the strength of the relationship when the animals were in and out of night-time retreats is shown in Table 6.8.

Emergence from night-time retreats was always associated with increase in T_a (Figures

6.18a-21a), however, the data in Table 6.8 show that air temperature can not always be closely associated with reptile Tb during active periods, especially on clear days, despite its wide acceptance among ecologists for this purpose. For example, animals will sometimes emerge at relatively low temperatures (e.g. 5.3°C at Lake St. Clair in October, 8.7°C at Egg Island, 11.01.92) and T_a does not indicate potential Tb as demonstrated by modified climate space using Ta (Figures 6.23-24). This is because T_a is just as much a dependent variable of the radiation regime as is Tb and will closely correlate with the latter for this reason.

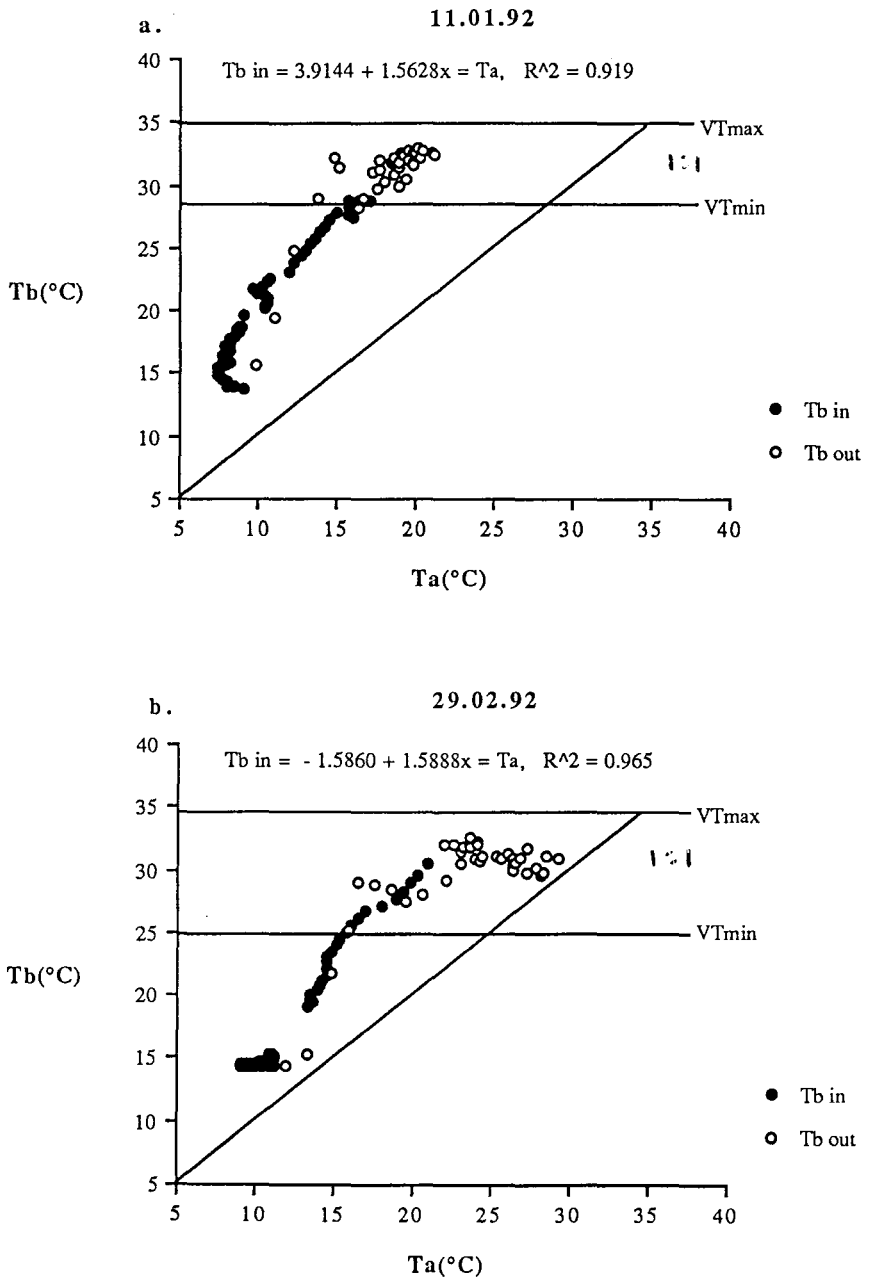


Fig 6.23 Modified climate space showing the relationship between Tb and Ta, on earthen pads (a) and on grass pads (b)

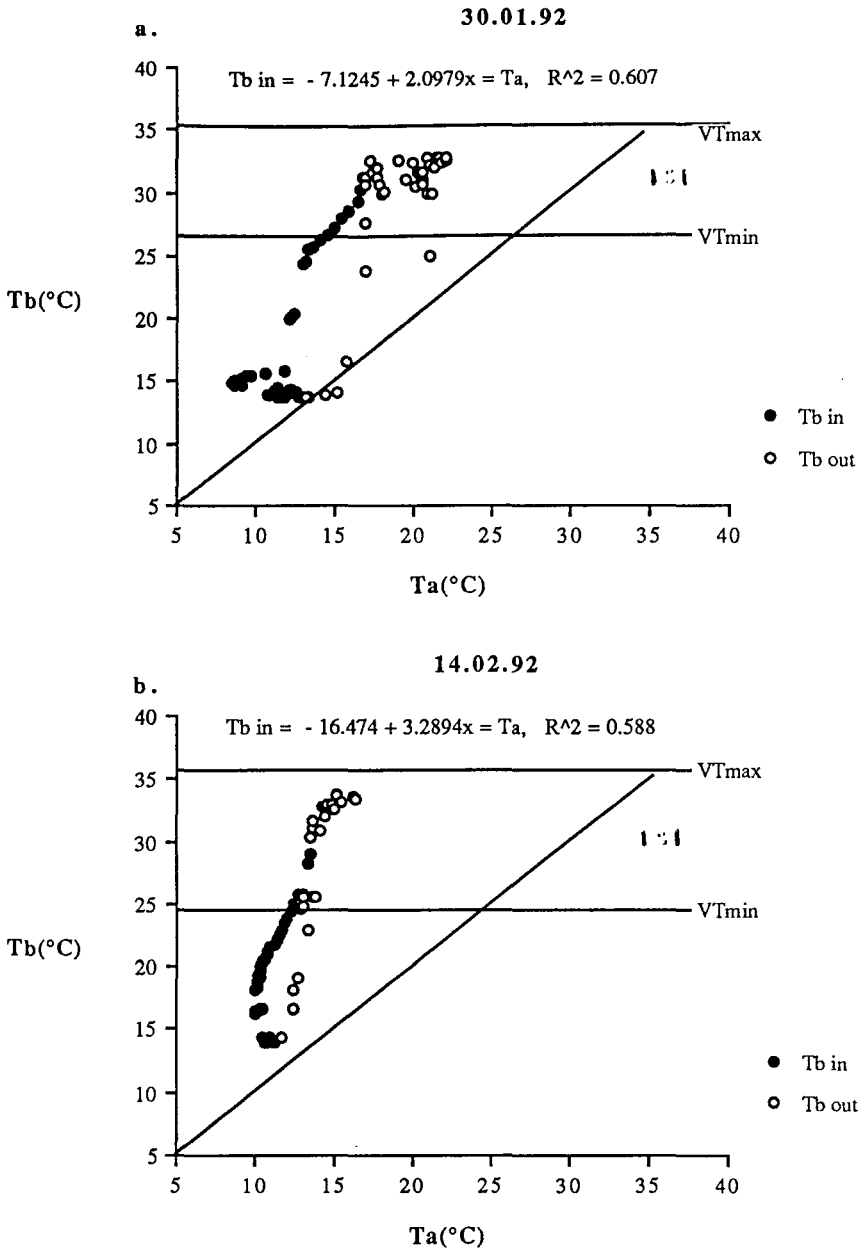


Fig 6.24 Modified climate space showing the relationship between Tb and Ta, on earthen pads (a) and on grass pads (b)

6.7 WIND SPEED AT SNAKE HEIGHT

Figure 6.26 shows the absence of a relationship (r^2=0.125, n=66) between the wind speed at screen height (1.6m) and at snake height (2cm). Wind speed at two centimetres above basking snakes was almost invariably found to be $\leq 0.5 ms^{-1}$. The data presented are from twelve days (three consecutive days from each field study) spanning the two

month summer period. On only two occasions were Tiger Snakes seen on basking pads in wind speeds of >0.5ms^{-1} and on both occasions the snakes were in the process of moving off the pads. While both the wind speed and direction at screen height are important in describing the nature of the broader local climate it is clear that the snakes are selecting basking pads which are below the local vegetation roughness length (height) and so may be considered to be within a small but discrete surface boundary layer. Thus the model assumption that the animals do not undergo forced convection on the pads is valid. Also, this suggests the screen air temperature may not always be a reliable predictor for Tb except when the local surface boundary layer is strongly coupled with the boundary layer above (i.e. at screen height, Table 6.8). Turbulence from above will occasionally penetrate through to snake height but the principal is clear: the snakes chose sites which minimise their exposure to forced convective conditions.

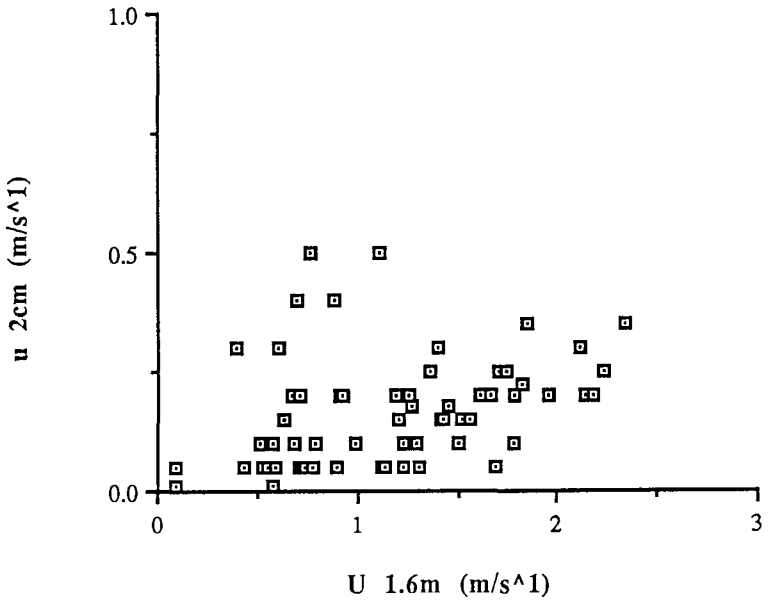


Fig. 6.25. Wind speed at snake height (2cm) and at screen height (1.6m).

6.8 SUMMARY

The non-gravid snakes for each elevation had similar eccritic mean temperatures and voluntary thermal limits. The mean at sea-level was higher than that at 830m. The maximum voluntary thermal limit was never observed for animals in the field. The gravid animals are a special case, having similar temperatures in spite of their different elevational origins.

Incoming radiation is a very strong predictor of snake Tb when the animal is out of the night-time retreat. Both K↓ and K↓ + L↓ are effective but K↓+L↓, i.e. combined global and thermal incoming radiation, is best for all conditions.

Ground heat flux, Q_g is always difficult to measure due to local surface heterogeneity and changing sky view effects. Q_g was a reliable indicator for the time of snake entry to night-time retreats from earthen basking pads but less so from tussock basking pads. If the animals are actively selecting basking sites to maximise their thermal opportunities then at different times they will select different pads. Q_g therefore will be an unreliable predictor of Tb if the animals are not using earthen basking pads. Q_g was never a good predictor of time of emergence.

Cloud cover is a persistent but variable feature and affects the snake Tb's. In part, using K↓+L↓ as predictors of Tb avoids the variation of Tb associated with cloud cover.

The sea-level animals are active in the rain, while those at the Lake Crescent were not. Precipitation events are associated with reduced T_a, K↓ and L↓ and so the animals at sea-level were basking between showers in an attempt to reach eccritic temperature. Those at Lake Crescent probably were experiencing very low radiation levels during rain and would thus not even attempt to bask.

The snakes select basking pads which are in general the warmest surfaces available early in the morning and late in the afternoon, dependent upon wind direction and speed. They do use pads which are sub-optimal but these are located close to the mouths of the night-time retreats and are used only briefly before moving to more suitable pads. Also it was clear that the animals select to avoid their voluntary thermal maximum and so could not be found on basking pads when $T_r \geq 35°C$, although as the pads cooled during the afternoon the animals would re-emerge onto the basking pads as $T_r \leq 35°C$.

The inground temperature at 5cm was a good predictor of Tb when the animals were in the night-time retreat. T_g at 20cm was very poor and since T_g at 2cm varied closely with T_a it was not a good predictor of snake Tb when the animal was in the burrow. The animals descend into the burrows when the T_a and T_g are both falling and usually when $T_a < T_g(5cm)$.

Emergence from night-time retreats was always associated with increasing T_a, but this varied so widely that a clear relationship for either time of emergence or body temperature

could not be derived.

The data for wind speed at snake height and screen height validated the assumption that the animals were not experiencing forced convection and suggested that they were indeed choosing sites to maximise thermal opportunity. Also the wind data suggests the reason for the poor performance of T_a in predicting Tb.

Other measured variables, e.g.. RH and wind direction , were not found to be related to Tb.

7 MODEL PERFORMANCE AND CONCLUSIONS

7.1 INTRODUCTION

In Chapter 1 the question was posed: is it possible to model Tiger Snake activity based solely on microclimatic parameters and energy budget analysis in Tasmania, and if so are these models adequate for predicting Tiger Snake behaviour?

This chapter outlines those microclimatic conditions which are associated with retreat-sites and basking-site selection, and the behavioural thermoregulatory response of Tiger Snakes to micrometeorological variation. In the following, Section 7.2. Empirical Relationships deals with those variables and quantities associated with emergence, those which determine the time required for daily warming, those which allow animals to freely move about the home-range, and those which trigger re-entry. Section 7.3 Biophysical Relationships discusses the analysis of the snake's energy budget and presents the results of the integrated parameter model. Section 7.4 Integration combines the results into a form which predicts snake thermoregulatory behaviour for three different weather conditions. Section 7.5 concludes the thesis with suggestions for future research.

7.2 EMPIRICAL RELATIONSHIPS

From the results in Chapter six it was attempted to derive simple empirical relations for each of the micrometeorological variables and Tiger Snake Tb. The following observations pertain only to non-gravid females.

7.2.1 Predicting emergence

From the study, T_g(5cm) was a good predictor of Tb when animals were in night-time retreats. T_g(2cm) varied closely with T_a and snake Tb was only rarely correlated with T_g(20cm). On every occasion recorded emergence followed an increase in T_g(5cm) and, due to the delayed increase in T_g(5cm) relative to T_a and T_g(2cm), the time of emergence was more closely associated with this variable than with any of the other variables measured (Figures 6.18a-21a). Q_g was discarded in favour of T_g because it is a difficult flux to measure or estimate for any point.

From the above, emergence occurs when T_g(5cm) as began its daily increase although the temperature at which this will always occur remains unknown.

7.2.2 Predicting Tb by Incident Radiation

Incoming radiation is a very strong predictor of snake Tb when the animal is out of the night-time retreat. Of the incoming radiation variables, K↓ and L↓ were found to have highly significant relationships with Tb (Section 6.4). Overall K↓+L↓ was found to be a stronger predictor of Tb than K↓ on its own. However, cloud effects and ground characteristics determine which form of radiation (total incoming or global) will be the stronger predictor. K↓ is a stronger predictor on its own on vegetation and as this is a more likely scenario for Tiger Snake basking pads in Tasmania it was selected as the radiation index of Tb. However, the index is weakened in cloudy conditions and is unreliable on rainy days. Empirical values for K↓ and Tb as determined by the study are given below. The value K↓ is used in the absence of L↓ as its measurement only requires one instrument (a pyranometer) and because of the infrequent availability and use of pyrgeometers. Further, availability of satellite data for K↓ makes its use more practical for regional comparisons.

From the above, the plotted values for K↓ show an approximate relationship between the quantity of K↓(Wm^{-2}) and Tb:

if $300 < K\downarrow < 400 Wm^{-2}$ then $Tb \approx 25\text{-}30°C$

and

if $400 < K\downarrow < 500 Wm^{-2}$ then $Tb \approx 30\text{-}35°C$

It follows that as VT is always less than 35°C the snakes will be at eccritic temperatures at or a short time following $K\downarrow \geq 400 Wm^{-2}$. As K↓ is dependent on time of day and day of year and then is further moderated by cloud amount, snake Tb is dependent upon cloud cover during summer when K↓ can be $\geq 400 Wm^{-2}$ for most of the day. However, this relationship does not pertain to the gravid female who was observed on several occasions to purposely slow her rate of Tb increase as it approached 30°C by moving off into shade.

7.2.3 Predicting surface movement by T_r

Tiger snakes select basking pads which are in general the warmest surfaces available early in the morning and late in the afternoon, dependent upon wind direction and

speed. When active through the day, these animals avoid their VT maximum, so they will not be found on $T_r \geq 35°C$ and will instead be located on sites with $T_r \leq 35°C$ (usually in the shade of a rock, log or low vegetation at 30-33°C). Thus snake activity will be increased on days that allow them to reach and maintain their eccritic Tb's and where the T_r's of their environments remain relatively cool. Such days in Tasmania in summer are usually overcast and often with high-level cloud.

7.2.4 Predicting entry into night-time retreats by Q_g

From Chapter six, Q_g was not found to be a good predictor of time of emergence in any situation, however, Q_g is a reliable indicator of entry into night-time retreats in open habitats. The relationship for snakes entering burrows is however only pertinent to burrows located on earthen/ground litter sites relatively free of vegetation. It is not a reliable predictor of entry for snakes living in tussock grassland situations (Section 6.4, Table 6.4) as a consequence of increased surface heterogeneity and changing sky view effects.

Based on these findings, Tiger Snakes enter night-time retreats when Q_g is approximately equal to or less than zero, but this is only relevant in the absence of rain.

7.2.5 Predicting location by wind

The data for wind speed at snake height and screen height validated the assumption that snakes do not experience forced convection while basking and suggests that they choose sites to maximise thermal opportunity. This thermoregulatory behaviour allows limited predictability of the choice of basking-site as animals will attempt to minimise exposure to wind during the warming phase.

Based on the above observations, Tiger Snakes will be located on the lee-side of convective shields in positions which allow them maximum solar opportunity.

From the above discussions it is plain that different aspects of Tiger Snake activity can be reasonably predicted from microclimatic conditions. The gravid animals are a special case and warrant further investigation.

7.3 BIOPHYSICAL RELATIONSHIPS

From the results in Chapter six, and based on the observations outlined above, the

following model assumptions are considered to have been validated.

7.3.1 Validation

Female Tiger Snakes maximise their thermal opportunities during daily warm-up phase by orienting their bodies and displaying thermoregulatory behaviour which maximises thermal uptake. Therefore, the model assumptions that Tiger Snakes will orient their bodies at an angle normal to the sun's rays, and flatten bodies in order to maximise thermal uptake, are considered valid. The model assumption that Tiger Snakes adopt an open posture during initial warm-phase was confirmed through observation and is also considered valid.

Tiger Snakes minimise their exposure to wind by taking advantage of available convective shields, therefore, the model assumption that Tiger Snakes are experiencing only free convective heat exchange is valid.

Their Tb's approximate inground temperatures at five centimetre depth at the time of emergence from night-time retreats and so the model assumption that Tiger Snake Tb equals T_g(5cm) is also valid.

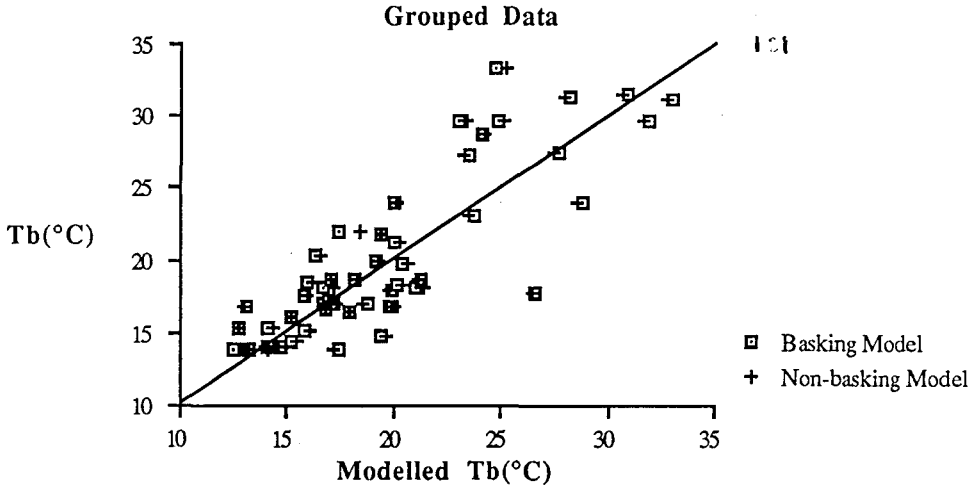


Fig.7.1 Grouped data sets showing the slight advantage of the non-basking sub-model over the basking sub-model in the models ability to predict Tb.

7.3.2 Model performance

As described in Chapter three, the model is radiation driven. The model's predictive ability was tested against measured rates of Tb increase, using Pearson's r correlation

coefficient, in basking and non-basking postures. Data sets selected for this purpose included complete ten-one hour basking periods beginning on the next quarter of the hour immediately following the emergence from night-time retreats. Tests were conducted on grouped and ungrouped data, which included: clear sky (c≤10%) against cloudy skies (c>10%), and non-gravid females against the gravid female (Table 7.1).

Table 7.1 Correlation matrix for Egg Island measured Tb's and modelled Tb's in basking and non-basking postures

TEST GROUP	EQUATION (TB=)	r^2	r	n-2	P
GROUPED DATA	2.05270+0.91571(BASKING),	0.705,	0.840,	48,	P<0.001
	1.43+0.94273(NON-BASKING),	0.718,	0.847,	48,	P<0.001
NON-GRAVID FEMALES	-2.133+1.1768(BASKING),	0.721,	0.849,	38,	P<0.001
	-2.6691+1.1953(NON-BASKING),	0.733,	0.856,	38,	P<0.001
GRAVID FEMALE	-2.099+0.98802(BASKING),	0.837,	0.915,	8,	P<0.001
	-2.0002+0.99125(NON-BASKING),	0.836,	0.914,	8,	P<0.001
CLEAR SKIES (CLOUD≤10%)	0.58574+0.93093(BASKING),	0.777,	0.882,	13,	P<0.001
	0.60065+0.93709(NON-BASKING),	0.777,	0.882,	13,	P<0.001
CLOUDY SKIES (CLOUD>10%)	-1.6997+1.1517(BASKING)	0.648,	0.805,	33,	P<0.001
	-2.0856+1.1596(NON-BASKING)	0.664,	0.815,	33,	P<0.001

The results (Figures 7.1-3) are all highly significant (P<0.001) and show that a minimum of 65% and a maximum of 84% of the variance can be explained by the model. Both the basking and non-basking sub-models show no or very little difference in their ability to predict Tb under cloudless conditions, or for the gravid female. The non-basking model shows a slight advantage over the basking model for the grouped, non-gravid and cloudy sky data.

Based on the superior performance of the non-basking sub-model, an attempt was made to improve the value of r^2 for the grouped and cloudy sky data by varying the assumed values for snake albedo and overall thermal conductance by five percent each. Results presented in Table 7.2 show a decreased variance from 0.733 to 0.716 for both when albedos where increased and decreased. This had a maximum effect on modelled Tb of ±0.02°C. These data suggest $0.132<\alpha s<0.146$ and support the assumed snake albedo value of 0.139.

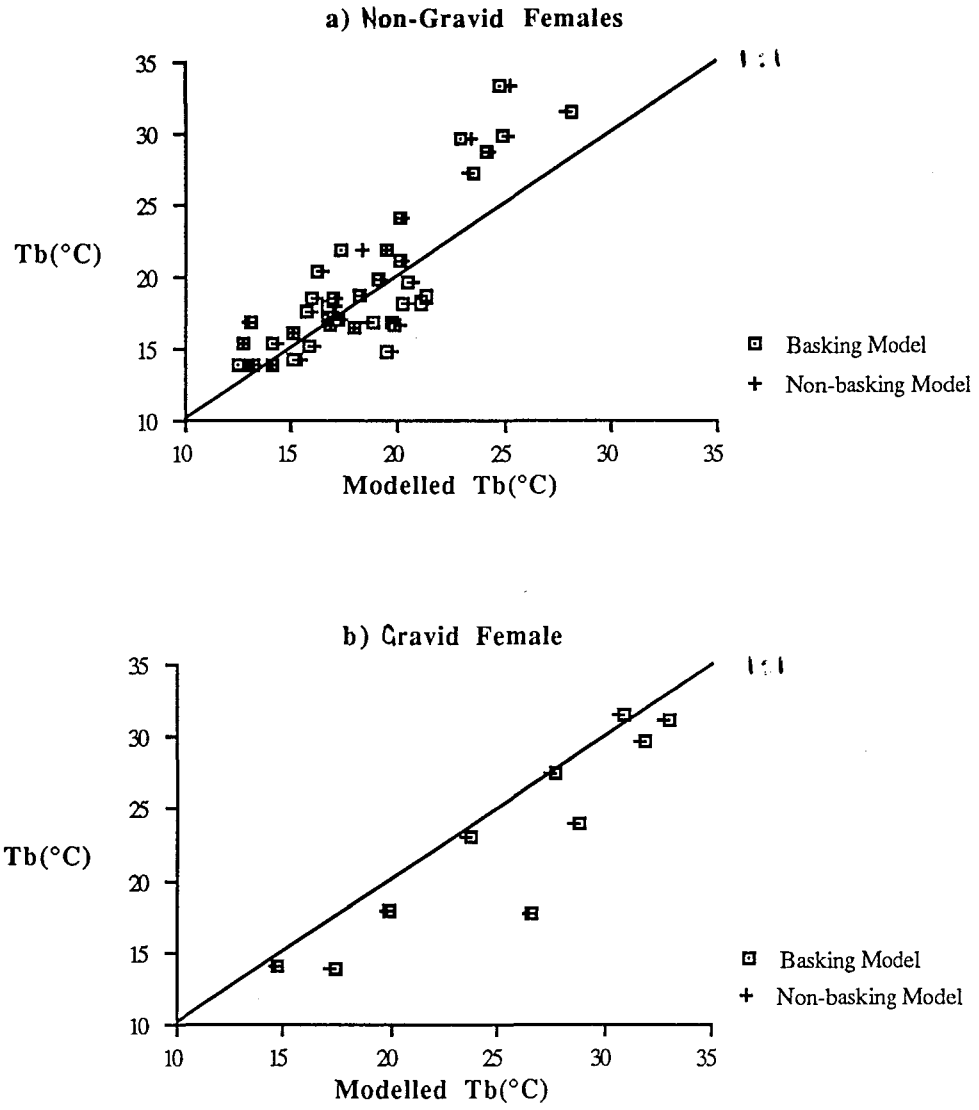


Fig.7.2 Modelled Tb against measured Tb for (a) non-gravid and (b) gravid females

Table 7.2 Correlation matrix for modelled non-gravid female Tb's in non-basking posture, where the assumed values for snake albedo were varied plus and minus five percent

EQUATION (TB model =)	r^2	r	n-2	P
-2.6080+1.2000(albedo = 0.132)	0.716,	0.846	38,	P<0.001
-2.6691+1.1953(albedo = 0.139)	0.733,	0.856,	38,	P<0.001
-2.6114+1.2008(albedo = 0.146)	0.716,	0.846,	38,	P<0.001

The models performance was not altered by changing the overall thermal conductance.

The model's inability to distinguish between postures, or the slight bias towards the

non-basking postures, and the high level of significance, are indicative of the model's dependence on the radiational environment rather than on physiological or behavioural adjustment. Varying the assumed snake albedo and body tissue thermal conductance had little or no effect, which further suggests the models independence of any biological response.

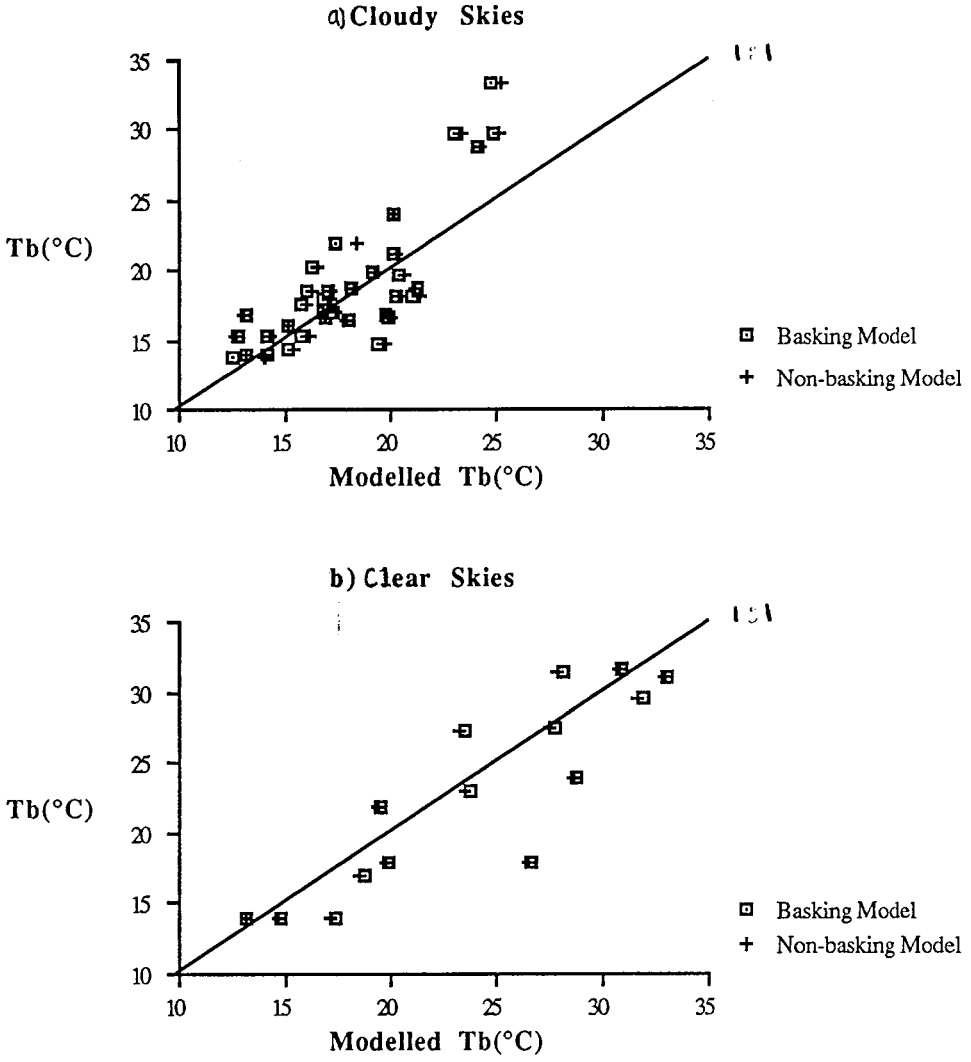


Fig.7.3 Modelled Tb against measured Tb for (a) cloudy skies and (b) clear skies

The results showed that the animals are capable of achieving higher Tb's than the physical model was able to predict, the exception being the non-gravid female which was over-predicted due to her habit of leaving basking-pads before reaching the laboratory determined mean eccritic temperature. This is taken to be a strong indication of the non-gravid animal's ability to maximise thermal uptake even when in low-energy environments. Tiger Snakes are therefore highly efficient absorbers of all forms of radiation. This suggests an inadequacy in the model in that it is not accounting for physiological or behavioural adjustment by the animal. A full integrated parameter model would take account of these factors and thus could be expected to give a more

accurate interpretation of Tb increase by the animal. Clearly the model is not complete and more work is required in these areas.

The model treats the snake as an environmental thermometer and, while both this method and physical models neglect any physiological response, the integrated parameter method used may have an advantage in that it is the animal which is determining its position within the environment. However, due to the absence of mechanical models for comparison this is only inference.

The value of the model lies in the assumption that it is representative of the true radiation budget of the animal. However, the values for snake surface albedo and emissivity, body tissue heat capacity and conductance, are assumed. Variability in solar load may to a large extent be discounted as a source of error, as the data selected to run the model was only taken from animals which had uninterrupted solar exposure for a full hour. Further, any random errors due to pad surface temperature variability, and associated errors in heat conduction between the ground and the snake, and convective heat flux, are not known. The models predictive ability may in future be further increased if these factors can determined and more appropriate values included in calculation.

7.4 INTEGRATION

The following is a descriptive account of the behaviour of lowland Tiger Snakes in Tasmania in summer. It concerns the daily routines of females and how the routines is modified by weather conditions. For the sake of illustration a general case is presented for snakes living on both earthen and grass basking-pads. Most animals observed used three morning pads regularly, sometimes with a fourth and fifth pad used only intermittently depending on conditions.

The time of emergence depends on the weather conditions: if clear the animal will usually emerge early (often within two and a half hours after sun rise) depending on the burrows location in relation to the sun; if cloudy it may be up to one hour later again (most often within half an hour of clear sky emergence); if raining the time of emergence, if at all, will usually be late (sometimes several hours after clear sky emergence). The presence of a cold wind may delay emergence still further or prevent the animals from emerging at all.

Basking-pads used by Tiger Snakes in the late afternoon are usually different from

the morning sites and are located where the snakes can take advantage of the last of the suns rays. In the following, the clear sky scenario is discussed in detail in order to illustrate full use of an animal's habitat on Egg Island. Cloudy skies and rainy days illustrate the moderating effects of adverse conditions on the animal's use of its microhabitat.

It is important to realise that most basking-pads do not represent a single set of conditions; the pad often includes several microclimates and a number of these may be used at the same time by the snake.

7.4.1 Clear sky conditions

Generally, the behaviour of Tiger Snakes is more predictable on clear summer days than at other times due to the intensity of incident radiation. At Egg Island animals often emerge early and move to basking-sites while air temperatures are still far cooler than inground or body temperatures. The following is an hypothetical case but is describing real values.

The empirical model predicts that on clear sky days Tiger Snakes will emerge from night-time retreats when T_g (5cm) begins to increase (Figures 6.18a-21a). The animal may only spend a few minutes warming at the burrow entrance before moving to the first pad usually located within one metre of the burrow entrance. This pad is often not the warmest surface available but it is always sheltered on most sides from the wind. The length of time spent at the first pad will depend on the intensity of the radiation and on wind speed and direction. If it is a bright still day the animal may move immediately to a more exposed third and well used basking-site (foregoing stopping at a second) with an open sky view and East or Northeast aspect. However, if wind is significant (i.e.. turbulent), the animal will usually stop to bask at the second pad and the wind will determine the position and posture the animal assumes on the pad. The third pad is usually the one most often used as the snake often reaches it sometime before reaching eccritic temperature; animals were most frequently recorded to move between the second and third pad at Tb≥23°C. The distance travelled to this pad is often between 3-6m (or more) from the burrow entrance. On bright mornings the snake may reach this pad within five, but usually ten to twenty, minutes after leaving the burrow.

The integrated parameter model predicts that the animal will be at mean eccritic temperature within one hour of leaving the first pad (refer to Table 6.4: 11.02.92, 30.01.92 for measured temperatures of clear day animals on earthen and *Poa* grass

pads respectively). Ground surface temperatures will increase rapidly, depending on the surface material, and during January and February may be in excess of 60°C on earthen pads during the latter half of the morning, and in excess of 30°C on the grasses. The empirical model, based on VT's, predicts that the snake will avoid earthen of ground litter pads at such times and will be located on or under the grasses depending upon the activity it is engaged in and on its thermal status. At midday the animal may also need to avoid the solar exposed grass surfaces and snakes will be generally difficult to locate at such times. This situation will continue until the late afternoon as the snakes, which may have been hunting under the grasses or in the marsh during the mid-morning, often appear asleep and are sequestered underneath the overhanging vegetation of their day-time retreats. The cool of the late afternoon brings them out again as surface temperatures drop to <35°C and they may actively seek elevated Northwest or Western aspects in the absence of wind in order to catch the last few hours of sun. Female Tiger Snakes often bask together at this time (as do other elapids, Shine, 1991) as several converge from the surrounding area to warmer sites.

According to the empirical model entry into night-time retreats will occur as the angle of the sun drops to a point where Qg approaches zero or becomes negative. The point of entry being determined by wind gusts or cloud over the sun, if this should occur, or until shade covers the ground surface as the snakes will attempt to take advantage of any radiation available to them during this time of the day. The snake will have left the communal basking-site by this time and taken up position on the last of the days pads which is usually located within half a metre of the night-time retreat and is slightly elevated; but the use of this last pad is often only for a relatively short period (if used at all) before it enters for the night and this will depend on its rate of heat-loss.

The depth snakes descend into retreats may depend on the temperature differences between the snake and its environment and if the snakes are much warmer than the ground or air temperatures they may delay descent well into the night, until they have cooled sufficiently to avoid sharp increases in body heat loss.

7.4.2 Cloudy sky conditions

Possibly due to the unpredictability of short-term variation in radiation intensity on cloudy days the snakes can be at their most unpredictable at these times.

Cloudy mornings necessitate long basking periods, as animals must wait for sufficient

radiative energy to raise their Tb's. If accompanied by a cool southerly air flow (a common case in Tasmania) this often means that snakes will remain on the basking-pads nearest their burrows (often within one metre) for many hours. However, cloud on still days often results in Tiger Snakes venturing to more distant pads. As the intensity of radiation increases later in the morning, a break in cloud cover can result in rapid increase in Tb (0.5°C or more) and result in snakes leaving their pads; however, long overcast periods will see them return and they may need to shuttle on and off pads all day. A blanket of high-level cloud on relatively warm days with low wind speed can result in high levels of diffuse radiation and give adult snakes the opportunity to roam extensively and spend long periods hunting.

The presence of cloud does not prevent T_g (5cm) from increasing and the snake usually emerges a little later then on clear days. The integrated parameter model most often under-predicts the animal's Tb but the correlation shows the animal's inability to reach eccritic temperature for several hours. The length of time required will vary depending on cloud height and form. Cumulus cloud being the most unpredictable in this regard can allow the animal the energy it requires in just a few minutes. However, the high energy burst may not be detected by the model, which is using the fifteen minute mean values of the instruments. Animals usually do not enter night-time retreats early on cloudy days unless the cloud is dense and accompanied by cold air. Entry depends on the cloud type and amount as frequent cloud breaks will encourage the animal to bask. On entry Q_g will not always be negative at such times.

Cloudy skies are common and persistent in the region (Nunez, 1988), and as such they must be considered when attempting to model Tiger Snake activity. Cloud occurred on most days during the study as is evident as spikes in the radiant energy and Tb graphs in Figures 6.4a-11a. It is clear that cloud cover directly effects the quantity and quality of incoming radiation and therefore influences snake thermoregulatory behaviour (Table 6.5). Cloud cover was concluded by Dredge (1981) at Lake Crescent to have no effect on Tiger Snake activity. This finding is clearly unsatisfactory for the lowland snakes where the effects of cloud cover were real but cloud was not a good indicator of snake activity on its own. Therefore, it must be concluded from the limited evidence available that Tiger Snakes at higher elevation may be responding to cloud differently and will require further investigation.

7.4.3 Rain days

Rain days usually resulted in decreased numbers of snakes active on the surface, however, Tiger Snakes are active in the rain. Animals often emerge between showers

late in the morning especially if the air temperature is relatively warm. Their activity above ground is limited often to the immediate vicinity of the burrow and their activity periods are comparatively short (Fig.6.8).

Even on rain days with little radiant energy, T_g (5cm) is increasing at the time when the snake emerges. The integrated parameter model both under and over-predicts the animal's Tb due to the animal seeking shelter between showers, however, the correlation is within three degrees centigrade and the model shows the animals inability to increase its temperature over its environment, predicting a low Tb. Animals often enter night-time retreats in the mid-afternoon on persistently wet days, especially with wind, and not all recordings showed Q_g to be negative at these times.

7.4 SUMMARY AND CONCLUSIONS

The study has demonstrated that differences in eccritic body temperatures and voluntary thermal limits occur in Tiger Snakes from different elevations in Tasmania. This may explain the observed differences in seasonal activity between the two elevationally isolated populations. Differences in eccritic body temperature are not seen in the gravid females however, which suggests these females require similar physiologically optimal temperatures.

This study has shown that female Tiger Snakes optimise their thermal opportunity at sea-level in Tasmania. This is evident by: minimised exposure wind at snake height, by maximised exposure to incoming radiation at every opportunity during warm-up phase (even to the extent of basking on wet ground between showers), by basking on the warmest ground surfaces available during warm-up phase (morning and afternoon), by maximising body-heat retention through selecting situations which minimise temperature differences with environments (even if this requires them to remain exposed to the ground surface at night).

Elevational differences in thermal ecologies have been indicated which include: lower mean eccritic body temperatures and voluntary thermal limits at higher elevation in summer (which may favour maximal seasonal activity in the cooler spring and autumn months and which might explain observed differences in activity patterns); Tiger Snakes at high elevation travel less distance to reach suitable basking sites than snakes at sea-level (possibly as a consequence of a cooler, less predictable and seasonally extreme environment).

The study has indicated that females are more closely associated with particular home-ranges than are males on Egg Island; the largest females observed always held the thermally optimal sites. Gravid female Tiger Snakes thermoregulate more carefully than non-gravid females (indicated by slightly higher mean eccritic temperatures and by leaving basking-pads early on warm days).

The snakes select basking pads which are in general the warmest surfaces available early in the morning and late in the afternoon, which is dependent upon wind direction and velocity. They do use pads which are sub-optimal but these are located close to the mouths of the night-time retreats and are used only briefly before moving to more suitable pads. Animals selected sites to avoid their voluntary thermal maximum and so could not be found on basking pads when $T_r \geq 35°C$, although as the pads cooled during the afternoon the animals would re-emerge onto the basking pads as $T_r \leq 35°C$.

7.4.1 The models

This study has suggested that it is possible to model Tiger Snake activity based on microclimatic parameters and energy budget analysis in Tasmania.

The study found several microclimatic indices of snake Tb which have been used to develop an empirical model of Tiger Snake activity. Tg(5cm) was been determined to be a good predictor of Tb when animals are in the soil and especially just prior to emergence of animals from night-time retreats. Incoming radiation was found to be a strong predictor of Tb when animals were above ground, with both $K\downarrow + L\downarrow$ and $K\downarrow$ alone found to be effect. $K\downarrow + L\downarrow$ was the best predictor but due to difficulty of measurement $K\downarrow$ was used in preference. $\bar{u}$ will determine the site chosen by the snake for basking and will always be $\leq 0.5 m^{-1}$ at the pad. Snakes at sea-level avoid $T_r \geq 35°C$ during the day and will only move onto a surface as $T_r \leq 35°C$. Q_g is a reliable indicator for the time of snake entry to night-time retreats from earthen basking pads and less so for grass basking pads

The above indices are further modified by cloud cover which is a common occurence in Tasmania and affects snake Tb's. In part, using $K\downarrow+L\downarrow$ as predictors of Tb may avoid the variation in Tb associated with cloud cover; however, $K\downarrow$ is easier to measure and has a slight advantage over $K\downarrow + L\downarrow$ on vegetative pads.

The empirical model to predict Tiger Snake activity patterns with a reasonable degree of accuracy if allowing for individual choice by the animal and sexual and asexual

differences in behaviour.

The integrated parameter model used the assumptions validated above for T_g (5cm)=Tb at emergence and $\bar{u}$ =≤0.5ms^{-1} above the pads. Other assumptions which were validated in the study where an open basking posture and the body held normal to the sun's rays.

The model was tested for: grouped, gravid female/non-gravid female and clear skies/cloudy skies. All results were found to be highly significant ($P<0.001$) and showed a minimum of 65% and a maximum of 84% of variance can be explained by the model. Both the basking and non-basking sub-models showed none or very little difference in their ability to predict Tb under cloudless conditions, or for the gravid female. The non-basking model shows a slight advantage over the basking model for the grouped, non-gravid and cloudy sky data. Varying the snake albedo and tissue thermal conductivity had no or very little effect on its predictability. This, the high level of significance and the models inability to distinguish between postures are taken to be indicative of the models dependence on the radiational environment. The model has shown the snakes to be highly efficient absorbers of the radiational environment which are not limited in a low energy conditions. However, the model is not complete and will require further development to take account of its neglect of physiobehavioural response.

7.4.2 Suggestions for future research

It must be concluded that the models used here, in their present form, are not entirely adequate for predicting Tiger Snake behaviours. But they do make a reasonable and workable attempt to predict the daily activities for adults. However, observations have shown that juveniles may occasionally have increased activity when activity in adults is reduced; e.g. an occasion following several days of rain when numerous small Tiger Snakes appeared after several weeks absence when most adults were inside out of the cold. The results here pertain only to the size class studied and future models may address this age/size dependant behaviour.

The importance of T_r to the snakes behaviour requires a more detailed appraisal as this variable was predicting the potential Tb and location of the snake, and is an important source of thermal energy available to a thigmothermic species like the Tiger Snake. This study could not measure this variable in more detail than it did, however, if it were attempted again far more effort would be directed towards obtaining continuous surface temperatures in all parts of the habitat.

This study was coarse in its attempts to relate wind velocity and air temperature taken at screen height to conditions at the animal surface, i.e. measurements inside the surface boundary layer are far more appropriate to the animal. Detailed measurements at several levels would be required to investigate and describe the degree of coupling between the surface boundary layer and screen height.

The responses of the gravid females should be investigated with regard to hormonal controls of behaviour. Further, if this were done in combination with knowledge of the thermal requirements of gravid animals, it might be possible to use an integrated parameter model with behavioural responses to assess the reproductive status of females.

The use of more complex body shapes and volumes in such models should be attempted although the current model will probably not be significantly improved as seen in the results obtained above for the two simple shapes.

Finally, this modelling offers the potential to truly predict the distribution of Tiger snake populations in detail. Other distribution models can not approach the resolution offered by this method although the inputs for this model are so specific and are not routinely collected there is a long way to go before this becomes a reality. Initially the process requires a more intensive survey of the elevational differences in Tiger Snakes and of the two other snake species in Tasmania. Secondly, the major input variables need to be modelled accurately on a State-wide basis. Then the distributions of the different species of snakes in Tasmania may be amenable to detailed prediction.

GLOSSARY

Acclimation	short-term habituation of an organism to a different temperature which alters its thermal tolerance, induced by laboratory exposure to appropriate thermal conditions which mimic acclimatisation
Acclimatisation	seasonal physiological change to the organisms thermal tolerance
Activity range	that temperature range in which normal activities can be undertaken; e.g. feeding, courting, mating etc.
Aestivation	(L. *aestas*, summer) a period of inactivity in summer associated with a state of decreased body temperature and metabolic rate; it is distinct from hibernation in that it occurs in hot seasons of the year
Ambient temperature	the average temperature of the medium, outside of the boundary layer, in the immediate vicinity of the animal
Aves	(L. *avis*, bird) a class of vertebrates
Blackbody	a surface or an object that absorbs completely any radiation incident upon it and has perfect emittance
Cold hardiness	physiological mechanisms allowing for survival of the animal at subfreezing temperatures
Conspecific	belonging to the same species
Core temperature	"The mean temperature of the tissues at a depth below that which is affected directly by a change in the temperature gradient through the peripheral tissues" (Bligh and Johnson, 1973), reserved to define endotherm body temperature (see deep body temperature)
Critical thermal	CT_{min} and CT_{max}, critical body temperatures beyond which *limits* animals will eventually die, they are the points at which normal physiological functions will cease, are associated with cell necrosis and usually determined by the loss of righting response in an ectotherm
Deep body temperature	

	temperature at a point deeper into the body than the cloaca and including the thoracic and visceral organs, reserved to define ectotherm body temperature (see core temperature)
Eccritic temperature	selected body temperature
Ectotherm	an animal which is dependent on an external source of thermal energy and termed cold-blooded; however, the organism may be effectively warm-blooded through behavioural thermoregulation
Elapidae	Elapids, fix-fanged venomous terrestrial snakes with principly neurotoxic venom and belonging to the cobra family. All of the Australian vonomous land snakes are considered to belong to this group
Endotherm	(Cowles, 1940) deriving heat energy from metabolism and termed homoiothermic or warm-blooded
Eurytherm	(Gk. *eurys*, wide) organisms adapted to a wide variation of body temperature, or ectotherm occurring in a habitat with a wide range of ambient temperature
Gravid	female with eggs or pregnant
Greybody	an entity which neither has perfect absorption or reflection of electromagnetic radiation with a radiant emittance a fraction of blackbody radiant emittance (R) given by: $R = \varepsilon\sigma\,[Ts + 273.16]^4$ where: ε is the emissivity of the surface, σ is a proportionality constant (Stephan-Bolztmann's `constant) $= 5.673 * 10^{-8}$ W m^{-2}°K^{-4}; Ts is the temperature of the surface in degrees Centigrade; R is in watts per square meter
Heliothermy	thermoregulation by exposure to sunlight, a basking animal
Herpetofauna	reptiles and amphibians
Heterotherm	(Gk. *heteros,* different) thermoregulating endotherm in which daily or seasonal body temperature varies more than ±2°K.
Hibernation	(L. *hibernus*, wintry) a period of inactivity associated

with low ambient temperature and restricted food supply, and a state of decreased body temperature and metabolic rate; it is distinct from torpor in that it is relatively long-term

Home-range — foraging area; *alt.* territory

Homoiotherm — (Gr. *homoios* , similar) endotherm, having physiological mechanisms which function to maintain a relatively constant body temperature (±2°K) independent of ambient temperature; *alt* homeotherm, homoeotherm, homotherm

Home-site — area containing all retreat-sites and basking-sites of an individual reptile

Phylum — (Gk. *phylon*, race or tribe), a primary division of animals thought to be related; e.g. Chordata, sub-phylum Vertabrata

Poikilotherm — (Gk. *poikilos*, changeable) an animal with no physiological means of thermoregulation, may be termed a thermoconformer

Selected preferred temperature range

range of body temperatures maintained by an ectotherm in a laboratory controlled temperature gradient where conditions exist that affords an animal the opportunity to select a body temperature above or below its activity temperature range

Stenotherm — (Gk. *stenos,* narrow) an organism adapted to a narrow temperature range

Stephan-Bolztmann's law

states that the intensity of radiant emittance (R) from a surface is proportional to the forth power of the absolute temperature of the surface; in the form:

$$R = \sigma [Ts + 273.16]^4$$

where: σ is a proportionality constant (Stephan-Bolztmann's constant) $= 5.673 * 10^{-8}$ W m^{-2} $°K^{-4}$, Ts is the temperature of the surface in degrees Centigrade; R is in watts per square meter

Thermoconformer — an animal which makes no attempt to thermoregulate and the body temperature is allowed to vary with that of ambient temperature

Thermoregulator — an animal which maintains a body temperature within a specified and usually narrow range through behavioural or physiological means

Thigmothermy — thermoregulation through conductance

Torpor — a period of inactivity, triggered by low ambient temperature and restricted food supply, associated with a state of decreased body temperature and metabolic rate; it is distinct from hibernation in that it is relatively short-term

Voluntary thermal limits — environmental temperatures at which the animal will cease normal activities and seek an environmental heat source (V_{min}) or shelter (V_{max})

Vertebrata — vertebrates (L. *vertebra*, vertebra), those animals with a series of vertebra running dorsally from the head to, and including, the tail

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APPENDIX 1

THE QUESTIONNAIRE USED TO SURVEY POTENTIAL STUDY-SITES, RELATIVE POPULATION DENSITIES AND BEHAVIOURAL TRENDS IN TASMANIAN SNAKES

1. Have you seen snakes at more than one location? Yes / No

Please list the locations (be as specific as possible)

a._____
b._____
c._____

2. How many snakes were seen?

a. one / more than one
b. one / more than one
c. one / more than one

3. What type of snake, or snakes, were seen at the above locations(if the species is unknown please give the dominant colour, size and pattern)

a._____
b._____
c._____

4. Give the approximate date of each sighting

a._____
b._____
c._____

5. Give the approximate time of day for each sighting

a._____
b._____
c._____

6. Please indicate if the snake / snakes were basking when sighted

a. YES / NO / NOT SURE
b. YES / NO / NOT SURE
c. YES / NO / NOT SURE

Comments

_____

Your name and phone number

_____

APPENDIX 2

A DESCRIPTION OF THE CIRCUIT USED TO DEVELOP THE DIGITAL INTERVAL COUNTER

The audio output of the receiver was fed into an absolute value rectifier circuit to produce a single pulse which has the same duration and amplitude as the audio signal. This pulse is squared in a schmitt trigger and divided by two in a counter. The output of the counter is a pulse which goes high at the commencement of a signal and low at the commencement of the next one. Thus its width is proportional to temperature. This is used to gate a crystal controlled oscillator into a sixteen bit counter/latch. When the pulse goes low and the counter stops counting the sixteen bits are transferred to a VART in two eight bit bytes where they are converted to a serial data stream and fed to the computer. This occurs at 1200 Baud with no parity, one stop bit and eight data bits.

The two bytes are then recombined using the computer. The most significant byte is multiplied by 256 and added to the least significant to produce the same number stored in the sixteen bit counter. This number is inversely proportional to temperature as the audio pulse repetition rate increases as the temperature increases producing less time between signals and therefore are a smaller number. The crystal derived frequency of 1920Hz is used as an input to the counter as this is used for the Baud rate generator and was a convienient frequency in the circuit.

APPENDIX 3

BASIC PC PROGRAMME TO PROCESS BODY TEMPERATURE

This programme inputs data from the serial port and saves it to file:

```
100 REM
110 OPEN "COM1:1200, N, 8" AS #1
120 A$=INPUT$(1,#1)
130 B$=INPUT$(1,#1)
140 A=ASC(A$)
150 B=ASC(B$)
160 A=A*256
170 C=A+B
180 PRINT C
190 GOTO 120
```

APPENDIX 4

BASIC PROGRAMME TO COMPUTE A DIFFUSE RADIATION CORRECTION FACTOR FOR A SHADING-RING, USING THE METHOD OF IQBAL, 1983.

```
10 READ DAY  'DAY OF YEAR
12 PI=3.14159
13 DAYA=2*PI*(DAY-1)/365
14 DEC=-(0.006918-0.399912*COS(DAYA)+0.070257*SIN(DAYA)-
0.006758*COS(2*DAYA)+0.000907*SIN(2*DAYA)-
0.002697*COS(3*DAYA)+0.00148*SIN(3*DAYA))
15 READ W,R
16 REM WIDTH,W AND RADIUS,R OF SHADING RING
17 READ LAT
18 LAT=LAT*PI/180  'LAT OF SITE RADS
20 SAZ=-(SIN(DEC)/COS(LAT))
21 AZ=ATN (SAZ/(SQR(-SAZ*SAZ+1)))+PI/2
22 REM AZIMUTH OF SUN AT SUNRISE
25 PROD=(AZ)*SIN(LAT)*SIN(DEC)+COS(LAT)*COS(DEC)*SIN(AZ)
26 X=(2*W)/(PI*R)*PROD*(COS(DEC)*COS(DEC)*COS(DEC))
27 K=1/(1-X)
28 REM GEOMETRIC CORRECTION FACTOR K
30 REM EDIT VARIABLES HERE
31 DATA 9
32 REM DAY
33 DATA 80,400
34 REM W,R
35 DATA 43.0833
36 REM LAT
37 PRINT "GEOMETRIC CORRECTION K"
38 PRINT USING"ff.ffffff";K
40 PRINT "FOR CORRECTION FACTOR ADD"
41 PRINT "  +0.07 FOR CLOUDLESS SKIES"
42 PRINT "  +0.04 FOR PARTLY CLOUDY SKIES"
43 PRINT "  +0.03 FOR OVERCAST SKIES"
44 PRINT "  DAY"
45 PRINT USING"fff";DAY
```

APPENDIX 5

INTEGRATED PARAMETER MODEL PROGRAMME TO CALCULATE SNAKE BODY TEMPERATURE (IN BASIC)

```
1 KK=0:SIGMA=5.673*10^-8
2 LAT=-43.0833:LONG=147.0167:K=.502
3 P1=3.14159:AS=.139
5 DIM TIME (100),D(100),L(100),TG(100),TR(100),TA(100)
7 DIM DIR(100),P1(100),P2(100),P3(100),P4(100)
10 INPUT "Enter snake number -e.g.,2-5)";SN
12 PRINT:PRINT:PRINT
15 INPUT "Enter snake's posture; 1=basking, 2=non-basking";SP
20 IF SN=2 THEN GOSUB 1000
31 IF SN=3 THEN GOSUB 2000
32 IF SN=4 THEN GOSUB 3000
33 IF SN=5 THEN GOSUB 4000
35 PRINT:PRINT:PRINT
37 INPUT "Enter day of year";DAY
40 PRINT:PRINT:PRINT
45 INPUT "Name of data file";F$
47 PRINT:PRINT:PRINT
48 INPUT "What is value of ground albedo, e.g. 0.13?";AG: PRINT:PRINT:PRINT
49 INPUT "Name of output file";G$
50 OPEN "a:"+F$ FOR INPUT AS #1
51 OPEN "a:"+F$ FOR INPUT AS #2
53 PRINT #2, DAY,SN,SP
55 FOR Q=1 TO 200
57 INPUT #1,TIME(Q),KC(Q),L(Q),TG(Q),TR(Q),TA(Q)
58 KK=KK+1
59 IF EOF (1) THEN 70
60 NEXT Q
70 LONGA = LONG * PI/180
80 THETA =2! * PI * (DAY-1) / 365!
90 DEC =-( .006918 - .399912 * COS(THETA) + .070257 * SIN(THETA) - .006758
*COS(2! * THETA) +.000907 * SIN (2! * THETA)-.002697 * COS(3! *THETA) +.00148 *
SIN(3! * THETA)
100 EQ =((7.500001E-05+ .001868 * COS(THETA) - .032077 *SIN(THETA) - .014617*
COS(2! * THETA) - .040849 * SIN(2! * THETA))*229.18) /60
105 FOR T=1 TO KK
110 TST=(4 /60)*(150-LONG)+(EQ)+TIME (JJ)
```

```
115 H=15! * (12!-TST) * PI /180!
120 CZ = SIN (LATA) *SIN(DEC))+COS (LATA) * COS (DEC)* COS(H)
130 Z = ATN(CZ /SQR (-CZ * CZ +1!)) + (PI /2)
140 CAZ =(CZ * SIN(LATA) - SIN(DEC)) / (SIN(Z) * COS(LATA))
150 AZ = ATN (CAZ/SQR (-CAZ * CAZ + 1!)) + (PI /2)
190 DIR(T) = (KC (T) - D(T)) /CZ
210 R1 = PI / 4!
220 R2 = (7/8) * 2! * PI
230 R3 = PI /4!
240 R4 = (7/8) * 2! * PI
250 REM azimuth angles calculated
260 P1 (T) = SIN (Z) * COS (AZ) * COS (R1)
270 P2 (T) = SIN (Z) * COS (AZ) * COS (R2)
280 P3 (T) = SIN (Z) * COS (AZ) * COS (R3)
290 P4 (T) = SIN (Z) * COS (AZ) * COS (R4)
295 NEXT T
300 REM the heat budget equation is now solved for the sum of the 4 pieces
400 FOR JJ = 1 TO (KK -1 )
402 IF JJ = 1 THEN TB = TG (1)
404 TS = TB
460 TTA = (TA (JJ + 1 ) - (TA (JJ))) /90
462 TTG = (TG (JJ + 1) - TG (JJ)) /90
464 TDIR = (DIR (JJ + 1) - DIR (JJ)) /90
465 TP1 = (P1 (JJ + 1) - P1 (JJ)) /90
466 TKC = (KC (JJ +1) - KC (JJ)) /90
468 TD = (D (JJ + 1) - D (JJ)) /90
470 TL = (L (JJ + 1) - L (JJ)) /90
472 TTR = (TR (JJ + 1) - TR (JJ)) /90
473 TTIME = 10 /3600
474 D = D (JJ) : L = L (JJ) : TR =TR (JJ) : TIME = TIME (JJ) : P1 = P1 (JJ)
475 TA = TA (JJ) : TG = TG (JJ) : DIR = DIR (JJ) : KC = KC (JJ)
476 GOSUB 4000 : PRINT "**********************************"
477 FOR Z = 1 TO 89
478 TA = TA + TTA
480 TG = TG + TTG
482 TR = TR + TTR
483 TIME = TIME + TTIME
484 L = L + TL
486 D = D + TD
488 KC = KC + TKC
490 DIR = DIR + TDIR
495 P1 = P1 +TP1
500 GOSUB 4000
510 NEXT Z
520 NEXT JJ
540 GOSUB 6000
1000 L1 = .1105
1010 L2 = .2635
1015 MS = 345
1020 L3 = .2125
1030 TV = .0014
1040 TD = .0089
1050 IF SP = 1 THEN A1 = .0042 ELSE A1 = .0028
1060 IF SP = 1 THEN A2 = .0112 ELSE A2 = .0079
1070IF SP = 1 THEN A3 = .0112 ELSE A3 = .0079
1080 IF SP = 1 THEN A4 = .0063 ELSE A4 = .0045
1090 IF SP = 1 THEN V1 = .0005 ELSE V1 = .0012
1100 IF SP = 1 THEN V2 = .0068 ELSE V2 = .0098
```

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1110 IF SP = 1 THEN V3 = .0068 ELSE V3 = .0098
1120 IF SP = 1 THEN V4 = .0018 ELSE V4 = .0027
1125 IF SP = 1 THEN SA = .0976 ELSE A2 = .0932
1130 RETURN
2000 L1 = .10595
2005 MS = 318
2010 L2 = .25265
2020 L3 = .20375
2030 TV = .0014
2040 TD = .0086
2050 IF SP = 1 THEN A1 = .0039 ELSE A1 = .0026
2060 IF SP = 1 THEN A2 = .0103 ELSE A2 = .0072
2070 IF SP = 1 THEN A3 = .0103 ELSE A3 = .0072
2080 IF SP = 1 THEN A4 = .0058 ELSE A4 = .0042
2090 IF SP = 1 THEN V1 = .0004 ELSE V1 = .0011
2100 IF SP = 1 THEN V2 = .0062 ELSE V2 = .00899
2110 IF SP = 1 THEN V3 = .0062 ELSE A1 = .00899
2120 IF SP = 1 THEN V4 = .0017 ELSE V4 = .0025
2125 IF SP = 1 THEN SA = 8.959999E-02 ELSE SA = 8.560001E-02
2130 RETURN
3000 L1 = .10452
3005 MS = 302
3010 L2 = .24924
3020 L3 = .201
3030 TV = .0014
3040
TD = 8.500001E-03
3050 IF SP = 1 THEN A1 = .0038 ELSE A1 = .0025
3060 IF SP = 1 THEN A2 = .01 ELSE A2 = .007
3070 IF SP = 1 THEN A3 = .01 ELSE A3 = .007
3080 IF SP = 1 THEN A4 = .0056 ELSE A4 = .004
3090 IF SP = 1 THEN V1 = .0004 ELSE V1 = .0011
3100 IF SP = 1 THEN V2 = .006 ELSE V2 = .0088
3110 IF SP = 1 THEN V3 = .006 ELSE V3 = .0088
3120 IF SP = 1 THEN V4 = .0016 ELSE V4 = .0024
3125 IF SP = 1 THEN SA = .0868 ELSE SA = .0832
3130 RETURN
4000 IF TS < TA THEN TS = TA + .01
4006 G1 = 9.810001 * L1 * (10^4) * (TS - TA) / ((273.16 + TA) * 2.28)
4007 G2 = 9.810001 * L2 * (10^4) * (TS - TA) / ((273.16 + TA) * 2.28)
4008 G3 = 9.810001 * L3 * (10^4) * (TS - TA) / ((273.16 + TA) * 2.28)
4010 N1 = .5 * (G1^.25)
4012 N2 = .5 * (G2^.25)
4014 N3 = .5 * (G3^.25)
4016 Q1 = N1 * .026 * (TS - TA) /L1
4017 Q2 = N2 * .026 * (TS - TA) /L2
4018 Q3 = N3 * .026 * (TS - TA) /L3
4020 HV = (.5 * D) + (.5 * KC) * AG + (.5 * L) + .5 * (SIGMA * (TR +273.16) ^4) - (SIGMA *
(TS + 273.16) ^4)
4030 HA = DIR * P1 + L + D - DIR *P1 *AS - D * AS - SIGMA * (TS + 273.16) ^4
4040 S1 = HV * (2 * V1) + HA * A1 - Q1 * (A1 + 2 * V1)
4042 S2 = HV * (2 * V2) + HA * A2 - Q2 * (A2 + 2 * V2)
4046 S3 = HV * (2 * V3) + HA * A3 - Q2 * (A3 + 2 * V3)
4048 S4 = HV * (2 * V4) + HA * A2 - Q3 * (A4 + 2 * V4)
4049 S5 = (.502 / TV) * (TR - TB) * (A1 + A2 + A3 +A4)
4051 ST = S1 + S2 + S3 + S4 + S5
4055 TB = TB + (10 * ST ) / (MS * 3.435)
4060 TS = TB
```

```
4070 PRINT USING "###.##" ; TIME, TB, TS, TR, TG, TA, ST
4075 PRINT #2, TIME, TB, TR, TG, TA, KC, DIR, D, L, ST
4100 RETURN
5000 L1 = .11375
5005 MS = 375
5010 L2 = .27125
5020 L3 = .21875
5030 TV = .0015
5040 TD = .0092
5050 IF SP = 1 THEN A1 = .0045 ELSE A1 = .003
5060 IF SP = 1 THEN A2 = .0119 ELSE A2 = .0083
5070 IF SP = 1 THEN A3 = .0119 ELSE A3 = .0083
5080 IF SP = 1 THEN A4 = .0067 ELSE A4 = .0048
5090 IF SP = 1 THEN V1 = .005 ELSE V1 = .0013
5100 IF SP = 1 THEN V2 = .0072 ELSE V2 = .0104
5110 IF SP = 1 THEN V3 = .0072 ELSE V3 = .0104
5120 IF SP = 1 THEN V4 = .0019 ELSE V4 = .0029
5125 IF SP = 1 THEN SA = .1126 ELSE SA = 9.880001E-02
5130 RETURN
6000 CLOSE#1
6010 CLOSE#2
6030 INPUT "Do you want to read another file?";A$
6040 IF A$ = "n" OR A$ = "N" THEN GOTO 6050
6045 ERASE TIME, KC, D, L, TG, TR, TA
6047 ERASE DIR, P1, P2, P3, P4
6049 GOTO 1
6050 END
```